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GENETIC DIVERSITY OF BEAN LANDRACES
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GREGORY B. MARTIN

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M. Wayne Adams
Major professor

M. Wayne Adams

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GENETIC DIVERSITY
OF BEAN LANDRACES IN
NORTHERN MALAWI

By

GREGORY B. MARTIN

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ABSTRACT

GENETIC DIVERSITY OF BEAN LANDRACES IN NORTHERN MALAWI

By

GREGORY B. MARTIN

The observation that diverse bean mixtures (*Phaseolus vulgaris* L.) are maintained by Malawian farmers prompted this study into the extent, the underlying patterns, and the generation of variability in this species in northern Malawi. The outcrossing rate, estimated by using flower color and hypocotyl pigmentation as dominant gene markers, was found to be 0 - 2.23%. Considerable variability both within and between landraces was documented for numerous phenological, morphological, agronomical and qualitative characters. A principal components analysis revealed a clinal pattern, with the northern and southern areas forming the extremes. Several statistically significant correlations were found between environmental variables and plant character measurements, suggesting that site-specific adaptation is occurring. Separate principal component analyses of each landrace revealed genetic intergradation involving major seed classes in these bean mixtures. It is postulated that a low level of outcrossing exerts a profound impact on the generation and maintenance of variability in the Malawian bean landraces.

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PROLOGUE

The common bean, Phaseolus vulgaris L., is a cosmopolitan species. It grows throughout Latin America, from the Andean highlands to the hot, dry plains of northern Mexico. Beans are an important cash crop in Michigan, California, New York, Colorado, Nebraska, Idaho, North Dakota and Minnesota. In recent years their production has increased in Canada. But beans are not confined to the New World. They are cultivated throughout Europe and are found in the Eastern African highland areas from Ethiopia to South Africa. This wide range is directly attributable to the tremendous genetic diversity encompassed by this species.

Beans were first domesticated in Latin America. Three theories exist regarding their origin. Miranda-Colin (1967) and Gentry (1969) believe that beans were domesticated in the Mexico-Guatemala region of Mesoamerica. However, Berglund-Brucher and Brucher (1976) have presented evidence for a South American (Andean) origin. Kaplan (1981) believes the archaeological record supports an independent origin in each of these areas. Beans were disseminated into the American southwest at least 2300 years ago and were in the northeast by 1000 A.D. (Kaplan, 1971). By the time of Columbus, beans had been established in North America for over 1500 years. According to Baker (1971), there is no evidence for a pre-Columbian dispersal of beans to the Old World.

In 1498, Vasco da Gama, the Portuguese explorer, first made contact with the Eastern African coast (Binns, 1976). During the next 60 years, Portuguese traders called at the ports of Sofala, Mozambique, Zanzibar and Mombassa (Oliver and Mathew, 1963). Although the Portuguese rarely ventured inland, their influence was carried to the interior by the Arab slave traders and Swahili merchants active in the region (Merril, 1954). This influence consisted of European and Asian goods, and most significantly, of many new food plants from Latin America. Merril (1954) states, "There is no doubt that the people who brought maize into Nyasaland (now Malawi) were Arabs of the coast. This community is known as 'Manga', which in Swahili means 'Arabia'". The Malawians today still refer to maize as 'Chi<u>manga</u>'.

By the early 1500's beans had been established in South America for several thousand years (Kaplan, 1971). The Portuguese, having established an outpost in Brazil, likely carried beans from this area during their voyages through the Indian Ocean. These voyages, besides promoting trade, were instrumental in setting up missions along the coast (Coupland, 1938). In 1542, St. Francis Xavier, on his way to Goa, visited missions at Mozambique, Malindi, and Socatra (Oliver and Mathew, 1963). These ports are within 150 miles of the lower Rift Valley in Malawi and the surrounding highlands. The highlands would prove ideal for many Latin American plant introductions, including beans. Several

Jesuit missions were founded in 1560 in what is now Mozambique (Coupland, 1938). These missions were likely an important catalyst to plant introductions in East Africa.

David Livingstone provides the first mention of beans in what is now Malawi. During his 1858-59 expedition along the lower Shire River, Dr. Livingstone recorded, "Many gardens of maize, pumpkins, and tobacco fringed the marshy banks as we went on ... and then the people brought meal, maize, fowls, batatas, yams, and <u>beans</u> for sale" (Livingstone, 1865). That beans were fully integrated into Malawian culture by the early 1900's is shown in the striking lexical diversity by which specific bean seed types were known (Williamson, 1975). Observations by the Malawi Bean/Cowpea Collaborative Research Support Project team in 1981-84 confirm this. Bean names may refer to seed color, (Kabaya = white), plant architecture, (Mwikala = "just sits there" - a non-climber), seed pattern, (Mwasipengele = spotted) and origin (Mine = from the Zambian copper mines). Such lexical differentiation has also been noted in beans in the municipio of Tenejapa, Chiapas, Mexico by Berlin, Breedlove and Raven (1974). They discovered that the degree of linguistic differentiation in a species is directly related to the importance of that species to the cultivator. This is consistent over both wild and cultivated plants. The common bean is known by at least six different names in Tenejapa, whereas a culturally unimportant species, <u>Clematis</u> <u>dioca</u> L., is grouped with several other Clematis species (and even other genera) under a common name.

Thus the remarkable array of local names given to beans in Malawi indicates that the farmers perceive qualitative (and perhaps quantitative) differences between genotypes <u>and</u> that these differences are culturally important.

This thesis is the result of a detailed study of the qualitative and quantitative variability in 15 bean landraces collected in the northern region of Malawi. Five hypotheses will be addressed:

1. There exists in the Malawian bean populations some degree of outcrossing. This outcrossing generates new seed types which often do not undergo selection by the Malawian farmers. The pollination vector(s) may be unique to Eastern Africa.

2. Extraordinary variability is present in Malawian bean landraces for many morphological, phenological, agronomic and qualitative characters.

3. The diversity within these landraces may lower the risk of crop loss and thus may have distinct advantages for the Malawian farmer.

4. There has been adaptation in these landraces to specific environmental variables such as soil nutrients, photoperiod, and altitude.

5. The populational structure of these landraces* is profoundly influenced by occasional outcrossing and the resulting recombination and segregation. Outcrossing in fact, may maintain polymorphisms in bean mixtures to a degree beyond even the farmer's intention.

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* The term 'landrace' is used in this thesis to refer to a heterogeneous mixture of a predominantly self-pollinating species which is maintained by a subsistence farmer. These mixtures, however, are much more than mere composites of pure lines. Rather, natural hybridization and recombination in a mixture result in the development of numerous "hybrid swarms". The differential adaptation of the segregants in such a swarm confers a genetic dynamism to these populations. The occurrence of genetic drift and individual farmer selection, as well as possible benefits both in performance and stability from their heterogeneity and homozygosity, serve to make each population genetically unique.

PART I

NATURAL HYBRIDIZATION
IN
MALAWIAN BEAN LANDRACES

Chapter 1

OUTCROSSING ESTIMATION

Literature review

The common bean (Phaseolus vulgaris L.), is considered to be a predominantly self-pollinating species. However, Rick (1950) has observed that "Intrinsic pollination relations of a species are often assumed to be the same under foreign conditions, but this is not necessarily the case". Since beans are an introduced species in Eastern Africa, the presence of unique and perhaps more effective pollinating vectors is entirely possible. Even with a fairly low rate of outcrossing, the potential for hybridization is significantly increased when beans are grown in genotypically complex mixtures as they are in Malawi.

The garden pea (Pisum sativum), commonly accepted to be completely self-pollinating, has been found to be 3.3% cross-pollinating in Peru - a region outside the native habitat of this species (Harland, 1948). Tomato (Lycopersicon esculentum), is highly self-pollinating in California but in its native habitat of Peru, some genotypes were found to be 40% cross-pollinating (Rick, 1950). The difference is thought to be due to the presence of several bee species which occur in Peru but not in California.

Darwin (1877), was probably the first to note cross-pollination in beans. He found that Phaseolus vulgaris L. was highly self-fertile, but that occasional outcrosses arose when black, white and brown-seeded beans were grown together. He remarked "The diversity of characters in the seedlings of the second generation was . . . wonderful".

Mackie and Smith (1935), working in California, grew out seed of individual plant selections of the California Pink bean (Phaseolus vulgaris L.). They found over 15% of the plants were heterozygous for seed color, size or shape. Between the homozygous lines a wide variation appeared in seed color and maturity date. In another experiment they planted alternating rows of white-seeded and color-seeded varieties. By scoring the recessive progenies for heterozygosity they estimated 0.73% outcrossing. However, they did not adjust for intra-genotypic crosses and since the varieties were planted in a 1:1 ratio their estimate should have been doubled: 1.46%.

Allard (1954) used four monogenically inherited gene pairs to estimate outcrossing in California lima beans (Phaseolus lunatus L.). He discovered rates between 1% and 15%, the difference being attributed to three factors: distance between rows, wind direction and varietal differences. Plant habit, growing season and different flowering dates had little effect on outcrossing.

In Alabama, Barrons (1938) estimated outcrossing in beans (Phaseolus vulgaris L.) to be between 2.63% and 8.26%. Outcrossing rates decreased as spacing between rows was increased. He found that outcrossing among bush beans was much lower (2.7%) than among climbing beans (5.11%). He attributed this to the longer flowering period of climbing beans.

Tucker and Harding (1975) scored 20,000 progenies of 12 common bean cultivars in Davis, California and found zero outcrosses. They calculated the maximum outcrossing rate which was compatible with their data, given the sample size, and found it to be 3.0×10^{-4}. They suggest that no isolation is necessary to obtain selfed seed at Davis.

Outcrossing is said to reach 30% in parts of Puerto Rico (Freytag and Vakili, 1977; pers. comm. to M. W. Adams) but this has not been independently confirmed. Carpenter bees are believed to be the vector. Antunes, da Costa, and Oliviera (1973) reported outcrossing rates of 6.2% to 10.6% in Brazil. They, however, did not adjust for allelic frequencies in their two experiments. When adjusted, based on their cultivar ratio's, their estimates range from 7.47% to 12.75%. If similar levels of outcrossing have existed over the past few hundred years, the beans introduced into Malawi from Brazil can probably be assumed to have consisted of some heterozygous seeds.

There are no published estimates of bean outcrossing in Eastern Africa. However, Stoetzer (1984) has recently reported that bean outcrossing in Ethiopia may reach 4.8%. He attributes the outcrossing to carpenter bees (Xylocopa spp.). Onim (1981a) has investigated pigeon pea outcrossing in Kenya and has found it to vary from 25.2% to 94.5%. The level of outcrossing was directly related to the number and activity of insect pollinators at each site (r = 0.994). Pigeon pea (Cajanus cajun L.) is considered to be an outcrossing species so these high estimates are not surprising. They do, however, clearly establish that effective legume pollinators are present in Eastern Africa. Onim (1981b) observed seven insect genera, comprising 24 species, pollinating pigeon peas in Kenya. Three genera: Megachile, Xylocopa, and Chalicodoma accounted for the majority of flower contacts. Williams (1977) counted on one Xylocopa and one Megachile individual respectively, in India, 5,500 and 107,333 pollen grains. Rick (1950) has observed bees in the Xylocopa and Anthophora genera pollinating tomatoes in Peru. These genera, along with Megachile, also occur in Malawi. Thus they appear to be present throughout the bean-growing regions of the tropics and are likely candidates for outcrossing activity.

Several investigators believe various species of thrips (Thysanoptera) are the primary pollinating vectors of beans (Mackie and Smith, 1935; Allard, 1954; Antunes et. al., 1973). Free (1970) observes "Thrips are able to enter legume flowers before they open and so may effect early pollination". Annand (1926) found six species of thrips in the 11 plant species which he observed. The average pollen grains per thrip was 5.8. However, large differences occured between thrips on different species: Acacia, 1 grain/thrip; Alfalfa, 2.3 grains/thrip; Lupin, 26.5 grains/thrip. He states that the pollination effectiveness of thrips depends on, 1) size of the pollen grains; 2) viscosity of the grains; 3) number and species of thrips present; and 4) the attractiveness of the flowers.

Attractiveness of flowers appears to be an important factor to bees as well. Leleji (1973) has studied the apparent preference by bees for different flower colors in cowpeas. He observed that bumble bees (Bombus spp.) preferred purple flowers over white flowers in a 3:1 ratio. Honey bees (Apis mellifera), however, preferred white flowers over purple flowers 2:1. These observations confirm that outcrossing by bees is not always a random process. If there is more intra-color than inter-color pollen transfer as these findings suggest, then outcrossing estimates based on flower color markers would tend to be underestimates.

The estimation of outcrossing rates play an important role in understanding the genetic structure and evolutionary dynamics of populations. It has been demonstrated that considerable variability may exist both within and between lines in self-pollinating species as a result of low levels of outcrossing (Allard, Jain, and Workman, 1969). In Malawi, beans are maintained in often exceedingly complex mixtures. The role of outcrossing in generating and maintaining this variability is a vital component to the understanding of the evolutionary dynamics of these populations.

INTRODUCTION

Beans (Phaseolus vulgaris L.) are maintained by Malawian farmers as extremely heterogeneous mixtures. These mixtures may consist of 20 or more different seed types. However, four or five seed types often account for 80% or more of the variability in many mixtures. The remainder is made up of "off-types", present in lower frequencies. These rare types are suspected to be the result of occasional outcrossing. If outcrossing is occurring in Malawi it could, in part, account for the striking variability which is observed in bean landraces in this country.

Rick (1950) has observed that "Intrinsic pollination relations of a species are often assumed to be the same under foreign conditions, but this is not necessarily the case". Since beans are an introduced species in Eastern Africa, the occurrence of different pollinating insects than are present in other bean-growing regions is entirely possible. Even with a fairly low rate of outcrossing, the potential for wide hybridization is significantly increased when beans are grown in complex mixtures as they are in Malawi. This study was undertaken to estimate the level of outcrossing which occurs among beans in Malawi. Observations and collections were made of suspected pollinating insects, and in the case of thrips, possible flower color preference was investigated. In addition, the segregation from one heterozygous seed, collected from a farmers field, was observed in order to quantify the number of seed types which may arise from outcrossing.

MATERIALS and METHODS

Two genotypes, differing in flower color, stem pigment, or growth habit were used in each of six isolation blocks (Table 1). Each line was increased for two generations in isolation in order to ensure homozygosity for the genetic markers. Purple flowers, purple hypocotyl, and indeterminant growth habit were used as dominant gene markers. In blocks 1, 2, 3, 4, and 6 the populations were formed by mixing 300 seeds of each genotype. The seeds were then sown randomly in 10 meter rows with 91 cm. between rows and 15 cm. between seeds within the rows. In block 5, the two lines were planted in alternating, 50 meter rows; spacing was the same as in the other blocks. All blocks were isolated from other beans either spatially (by at least 300 meters) or by flowering time. Block 6 was planted at Bembeke research station in Dedza district on 5 January, 1983; flowering occured in mid-Februaury. The other blocks were planted at Bunda College of Agriculture in Lilongwe district on 23 February, 1983 and the plants flowered in mid-April. No insecticides were applied from two weeks before until one week after flowering. Days to first

Table 1: Growth habit, flower color, stem color and days of flowering coincidence in the six populations.

Block	Line	Growth Habit *	Flower Color	Stem Color	Flowering Coincidence
1	C86-8	I	white	green	15 days
	C55-1	I	purple	green	
2	C61-4	IV	white	green	20 days
	C81-23	IV	purple	purple	
3	C86-8	I	white	green	11 days
	C81-23	IV	purple	purple	
4	C61-4	IV	white	green	10 days
	C55-1	I	purple	green	
5	P643	I	white	green	12 days
	Ntcheu Khaki	I	purple	green	
6	Seafarer	I	white	green	4 days
	Domino	II	purple	purple	

* Growth habit according to Singh (1981).

flowering and days to end of flowering were recorded for each line and the overlap was calculated for each population.

During flowering in blocks 1, 2, 3, and 4, notes were taken on the number of thrips in 25 randomly-selected flowers from each line. A t-value was calculated to test if the thrip number means differed on white versus colored flowers. Collections were made of insects observed visiting bean flowers. The thrip species was identified at the Commonwealth Institue of Entomology, London. The bees were identified at the Department of Entomology, Michigan State University.

Since the germination in blocks 1 thru 4 was uneven, the number of seeds produced by each line was calculated by dividing their yield by single seed weight, and the proportions were used as estimates of the dominant (p) and recessive (q) allelic frequencies. Stands were uniform in blocks 5 and 6 and allelic frequencies were assumed to be the same as the original seed proportions ($p = q = 0.5$).

The progeny of parents carrying the recessive allele from blocks 2, 3, and 6 were sown in sand flats where germination was virtually 100%. The frequency of heterozygotes as determined by those plants showing stem pigment was recorded. Progeny of recessive parents from blocks 1, 4, and 5 were sown in the field and the frequency of the heterozygotes was determined by flower color. Germination in the field was higher than 95%.

Outcrossing rates (t) were estimated using the method suggested by Jain (1979):

$$t = H / p$$

where H = the number of heterozygotes (a) divided by the total progenies observed (a + b), and p = the dominant allelic frequency. Jain (1979) gives the variance of this estimate (s^2) as:

$$s^2_i = \sum(t_i / (a + b)p) \cdot (1 - p / p).$$

Heterogeneity of the various t estimates was evaluated using the test-statistic given by Jain (1979):

$$\text{Chi-square} = \sum(t_i - t^*) s^2_i$$

where $t^* = \sum(t_i / s^2_i) / \sum(1/s^2_i)$, and chi-square has k - 1 degrees of freedom.

In block 3, Harding and Tucker's (1975) formula was used to calculate the maximum outcrossing estimate that is compatible with this sample size, given that no outcrosses were observed:

$$t_{max} = T_{max} / \ 1 - q - 2(q(1 - q) / k)^{1/2}$$

where $T_{max} = 1 - e^{(\ln(1 - p)) / N}$, q is the frequency of the recessive allele and k = sample size from which q was determined.

In a related study, the segregation was observed of a suspected heterozygous seed collected from a Malawian farmers' field. This seed, C110-24, was planted at East Lansing in the summer of 1982 and its selfed progeny were subsequently increased at Bunda College of Agriculture. In turn, progenies were grown from each of these plants. The various seed colors, shapes and sizes were recorded as an indication of the array of seed types which may arise from a single heterozygous seed.

RESULTS

With the exception of block 6, flowering coincidence was longer than 10 days in all blocks (Table 1). Outcrosses were observed in all but block 3 (Table 2). The maximum outcrossing rate compatible with the block 3 sample size, given that no outcrosses were observed, was calculated to be 0.0032% according to Harding and Tucker's method (1975). Rates of outcrossing varied from this low up to 2.23% in block 2. The average outcrossing rate for all blocks was 0.813%. The highest rate was observed where both parents were climbing beans and the flowering coincidence was longest. Standard errors were relatively small for all block estimates. The chi-square test for heterogeneity of estimates was not significant ($.25 < P < .50$).

Table 2: Estimates of outcrossing rates for the six populations.

Block	Total progeny scored	Number of Heterozygotes	Frequency of dominant allele	Outcrossing rate (t)	Standard error (s)
1	3295	6	0.466	0.39	0.017
2	6727	50	0.333	2.23	0.045
3	1502	0	0.635	0.003*	0.000
4	499	3	0.605	0.99	0.046
5	1062	4	0.500	0.75	0.038
6	4966	13	0.500	0.52	0.015

* Maximum outcrossing rate compatible with zero observed heterozygotes and sample size of 1502, according to method of Harding and Tucker (1975).

The insect collections revealed a diverse array of vectors (Figure 1). Thrips, _Megalurothrips_ _sjostedti_ Trybom. (det. J. Palmer) were present in the flowers of all blocks and indeed, are observed in bean flowers throughout Malawi. Seven bee species, from three genera, Anthophora (1 species), Xylocopa (3 species), and Megachile (3 species), (det. M. Arduser), were observed visiting bean flowers throughout flowering. Figure 2 depicts a female from the genus Xylocopa visiting a bean flower.

The thrip counts revealed no significant differences for flower color preference by these insects in the four blocks observed (Table 3). In addition, there was no significant correlation (r = -0.5487) between average thrip number per flower and the outcrossing rates for the blocks.

The segregation of C110-24 resulted in over 60 unique seed types based on color and pattern (Figure 3). The single seed weight ranged from 0.237 gms. to 0.562 gms. in the first generation and from 0.286 gms. to 0.771 gms in the second generation. Undoubtedly, many more types would have been retrieved had the progeny size been larger.

Bee genera - corresponding to Figure 1.

Xylocopa spp. (species 1) female	Xylocopa spp. (species 1) female	Xylocopa spp. (species 2) female	Xylocopa spp. (species 2) female
Xylocopa spp. (species 1) male	Xylocopa spp. (species 3) female	Xylocopa spp. (species 3) female	Megachile spp. (species 1) female
Xylocopa spp. (species 2) female	Anthophora spp. (species 1) female	Megachile spp. (species 2) female	Megachile spp. (species 3) female
Eumenine wasp	Xylocopa spp. (species 3) female	Xylocopa spp. (species 3) female	Cleridae beetle

(determinator: M. Ardeuser)

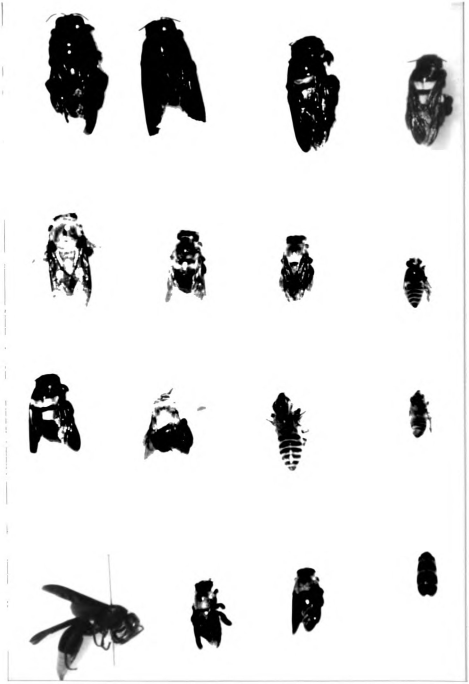


Figure 1: A collection of insects observed visiting bean flowers in Malawi.

(See key on facing page.)

Figure 2: A bee from the genus Xylocopa visiting a bean flower.

Table 3: Number of thrips per flower. Average of 25 random flowers of each color.

Plot Number	Flower color		Plot Average	t - value
	Purple	White		
1	1.80	1.64	1.72	0.35 ns
2	1.00	0.84	0.92	0.517 ns
3	1.24	1.56	1.40	0.745 ns
4	0.36	0.56	0.46	1.157 ns

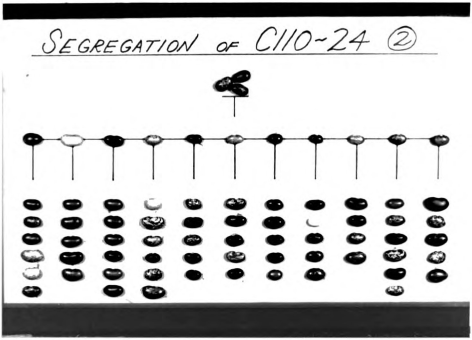


Figure 3: The array of new seed types recovered from the segregation of seed C110-24.

DISCUSSION

These experiments provide evidence that a low level of outcrossing is occurring in Malawian beans. Low to moderate outcrossing in beans has also been reported in the U.S.A. and Brazil. However, these countries grow homogeneous varieties of beans and the outcrossing thus would unite similar genotypes in most fields. In contrast, Malawian farmers often grow extremely heterogeneous mixtures of beans and an outcross is much more likely to unite dissimilar types. If only one genotype is growing in a field, as is often the case in an American bean field, then outcrosses are in effect equivalent to self-pollinations. If two types are present, in equal proportions, then the probability of an outcross uniting the two types is 50%. However, if 10 types are present in equal proportions the chance of uniting different types, should an outcross occur, is 90%. With 30 seed types the probability is 97%. Many farmers in Malawi maintain mixtures of 10 or more seed types, and while these are not present in equal proportions, the probability of joining dissimilar types remains very high. Thus a low level of outcrossing can have a magnified effect in complex genotypic mixtures. This fact, coupled with the wide array of seed types which may arise from just one outcross, as is shown by the segregation of C110-24, may provide a partial explanation of the seed diversity in Malawian bean landraces. Heterozygote advantage, if present, would increase the level of heterozygosity in these populations and raise the probability of heterozygotes being joined by outcrossing. Clearly, natural outcrossing, even at the low levels observed here, could be a potent mechanism for generating landrace variability.

Several authors have stated that outcrossing in beans is effected by certain species of thrips (Allard, 1954; Mackie & Smith, 1935). Thrips are observed in bean flowers throughout Malawi, however in this experiment the average number of thrips in a field did not correlate with the level of outcrossing. This suggests that other vectors are responsible for outcrossing. Three genera, comprising seven bee species were identified visiting flowers in the test plots. Two genera, Xylocopa and Megachile, are believed to effect cross-pollination of pigeon peas in Eastern Africa (Onim, 1981b). Large quantities of pollen grains have been observed on members of these genera in India. Another genus, Anthophora, also identified in the outcrossing test blocks, is known to be an effective tomato pollinator in Peru (Rick, 1950). These reports lend support to the hypothesis that the seven species observed from these genera may be the important pollinators of beans in Malawi.

The highest rate of outcrossing was observed in the test block comprised of two climbing bean genotypes. Barron (1938) observed twice as much outcrossing in plots combining two climbing types as opposed to two bush bean types. This rate may be due to the longer flowering coincidence of climbing beans. A longer flowering time may, perhaps, allow more pollinators to discover the field and visit the flowers. Since beans in Malawi are known to be 75% to 100% climbing types depending on the district, it may be that the outcross rates observed here, where only one plot included two climbers, are underestimates of the true outcrossing rates.

Preliminary data on heterozygosity levels from five Northern region bean-growing areas range from 2.3% to 46.7%. The average percentage of heterozygous plants per farm site was 17.3%. There is a positive, though not significant, correlation (r = 0.439), between frequency of indeterminate types and the level of heterozygosity. The high heterozygosity levels at these sites suggests either 1.) The present estimates of outcrossing rates are underestimates, or 2.) There exists some degree of heterozygote advantage for fitness.

PART II

DIVERSITY IN MALAWIAN BEAN LANDRACES

Chapter 2

GENETIC DIVERSITY IN LANDRACES

Literature review

Multivariate analyses, particulary principal component analysis and canonical variate analysis, of a complex of metrical and qualitative traits have been successfully used to establish diversity patterns in the germplasm collections of many crop species. Two approaches to this numerical taxonomic technique have been considered by Gilmartin (1967). One is the utilization of large numbers of characters on relatively few individuals, and the other deals with a smaller number of characters pertaining to large numbers of individuals. There is a continuum, of course, between these two extremes but to date most biologists have used the latter to study population structure, geographical variation, and infra-specific variability. Gilmartin suggests this approach be termed "quantitative taxonomy". A review of the application of various multivariate techniques to populations of several crop species should serve to clarify the information which can be expected through the use of quantitative taxonomy.

Goodman (1967) measured over 1000 plants belonging to 15 races of maize (Zea mays) indigenous to southeastern

South America. Sixteen morphological traits were observed, six pertaining to the ear, four to leaf size and number and the remainder to the length of various portions of the plant - peduncle, spike etc.. Using Mahalanobis' generalized distance, D^2, he clustered the races into groups which corresponded well with divisions based on classical taxonomic techniques.

Narayan and Macefield (1976) evaluated the world germplasm collection of 5477 line of chickpea (<u>Cicer arietinum</u>) for eight characters: plant type, flower color, days to flowering, days to seed maturity, pod size, number of seeds per pod, weight of 100 seeds and seed color. From the total collection they randomly chose 100 lines representing eleven geographical areas of the world. Utilizing Mahalanobis' D^2, they were able to cluster the populations into six groups, with plant type, seed color, and 100 seed weight contributing the most to total divergence. Interestingly, the lines from Mexico, where chickpeas were introduced by the Spaniards just 400 years ago, fell into a separate cluster. This is supportive of the view that human and natural selection under totally different agro-ecological conditions is such that considerable genetic divergence may occur over a relatively short evolutionary period.

Hancock and Bringhurst (1978) evaluated thirteen populations of strawberry (<u>Fragaria</u> <u>vesca</u>), from distinct ecological sites in California, for 25 quantitative traits and two enzyme systems. They were able to show, using analysis of variance and genetic identity techniques (Hedrick's Index, (Hedrick, 1971)), that considerable adaptation to specific environments had evolved. They concluded that Fragaria vesca is a "specialist" - a species of numerous variant ecotypes - which enables it to adapt to a wide range of ecological habitats. A discriminant analysis of 254 individuals belonging to three species of California strawberries assigned each individual to the correct taxon with a 99.61 percent success rate (Jensen & Hancock, 1982).

A Mahalanobis' D^2 analysis of days to flowering, days to physiological maturity, height, lodging, and grain yield of ten Durum wheat cultivars (Triticum turgidum L. var. durum), revealed no specific association between types from the same geographic area (Lee & Kaltsikes, 1973). The analysis did, however, clearly separate the cultivars into tropical (short-daylength), and temperate (long-daylength) clusters.

A study of 190 rice types from Assam and the northeast Himalayas and four standard varieties - three "indica" types and one "japonica" type - revealed considerable diversity among both existing cultivars and landraces (Vairavan, Siddiq, Arunachalam, and Swaminathan, 1973). Canonical analysis reduced the 190 types to 42 groups, and Mahalanobis' D^2 further reduced these to nine groups. The "japonica" type formed a separate cluster by itself. The three "indica" types were found in three separate clusters. A majority of the the primitive cultivars clustered with the "indica" types, however, several were intermediate between these and the "japonica" type and others were very close to the "japonica" type. This appeared to indicate that a series of intergrades bridging these two rice types has evolved in the northeast Indian rice populations.

Malhotra and Singh (1971), using D^2, were able to discern eight clusters among 25 strains of black gram (Phaseolus mungo Roxb.) collected from various geographic areas in India. Genetic diversity did not appear associated with geographic origin. They concluded that considerable diversity exists in this species in India.

A principal component analysis of 18 characters measured on 640 lines of finger millet (Eleusine coracan L.) revealed twelve broad groups as a result of plotting the first two standardized principal components (Hussaini, Goodman & Timothy, 1977). The lines from India showed clinal variation, with southern and eastern samples forming the extremes. Finger millets from Uganda formed two distinct groups, which were close together, but isolated from the other material. The authors suggested that the gap between these two groups from the same country may be due to a sampling error or may represent a true biological phenomenon. They stated further that "It is likely that natural geographical barriers, proximity to the equator, and associated climatic and ecological conditions may have restricted gene flow from adjoining areas. Perhaps of more importance is that distribution of crops in Africa is determined more by the influence of tribes and cultures than by ecological adaptation of plants (Harlan, 1975)". Interestingly, they found a resemblance between the millets from Africa and southern India, which they suggest may be the result of trade relationships between these two regions tracing back to the Arab slave trade.

Nevo, Zohary, Brown and Haber (1979) have studied 28 populations of wild barley (Hordeum spontaneum) collected from various ecogeographical areas in Israel. They concluded that wild barley in Israel is extremely rich genetically, but because of predominant self-pollination the variation is carried primarily by different homozygotes in the populations. This finding, in general, agrees with Imam and Allard's (1965) observations of wild oats in California. They, however, found that considerable variability may also exist within families in self-pollinating species populations under very low outcrossing levels. Nevo, et al. also found that allozymic diversity displayed clinal, regional, and local patterns which were often significantly correlated with environmental variables.

Distinct geographic variation for four morphological traits was observed between sites within areas and between areas.

Several workers have analysed limited sets of materials of the common bean (Phaseolus vulgaris). Rathjen (1965) identified five "botanical races" which he felt were genetically and physiologically distinct. Froussious (1970) evaluated 100 bean cultivars for adaptation to the growing conditions of England. He concentrated on characters which have agricultural value: determinancy or indeterminancy, number of internodes, seed size, pod characteristics and flowering behaviour, and arrived at four main plant types. Subsequently, these were modified by Singh (1981) to allow for subdivision according to pod load distribution, branch length and main stem strength.

Walters and Evans (1978) used a canonical variate analysis to study eight characters of bean lines from twelve countries. A plot of the first two variates revealed five distinct clusters. One cluster included varieties from Latin American countries (Guatemala, Colombia, Nicaragua, Mexico, and El Salvador) and another cluster consisted of lines from Turkey, Chile, Ethiopia, and the U.S.A.. Cultivars from Iran, Afghanistan, and Malawi each clustered separately, though in the same general area of the plot. The preponderance of climbing beans from these latter three countries was felt to be the reason for this separation.

Adams (1977) evaluated 22 commonly grown North American bean cultivars for a diverse set of agronomic and chemical attributes. Employing principal components analysis, he identified each cultivar, on the basis of 36 metrical traits, as a point in a standardized multi-dimensional space. Distances were then calculated between the cultivars and, after weighting by the acreage of each variety, an assessment of genetic vulnerability of the germplasm pool was obtained. The distances between varieties, based on the first six principal components, were significantly inversely correlated ($r = -0.68$) with the pedigree relationships estimated by Wright's path coefficient method.

Bassiri and Adams (1978), using banding patterns from just two polymorphic isozymes, peroxidase and esterase, successfully established the relationships between 34 U.S. bean cultivars which corresponded well with known pedigrees. More recently, Weeden (1984) used 10 polymorphic isozyme loci to discriminate among 88 cultivars of white-seeded snap beans. These polymorphisms allowed the unique identification of 60 percent of the cultivars.

To date, no study has been published on the extent and underlying pattern of genetic diversity in landrace populations of the common bean.

Beans are apparently maintained as mixtures throughout their center(s) of origin in the Andes (Kaplan, 1981; Zimmerer, 1984 personal communication) and in Mesoamerica (Kaplan, 1981). They are maintained also as mixtures in what may be termed their "secondary center" of diversity in Eastern Africa. These mixtures are composed of diverse seed types and, in general, fit Harlan's (1975) description of landraces:

> ". . . often highly variable in appearance. Landraces are adapted to conditions of traditional agriculture, they are adapted to low soil fertility, low plant populations, and low yield. Genetic variation within a landrace may be considerable, but it is far from random. The various component genotypes have survived in a region for a long period or they are offspring of lines that have undergone local selection for many generations. Landraces are built up and the components are selected, reassorted, recombined, and rearranged but the local materials are constantly being adjusted to local conditions".

Harlan (1975) has stated that the secondary center of many crops holds more diversity than the primary center, and that this diversity is generated as much by people as by ecological or climatic diversity. Stebbins (1957) reiterates this view for autogamous species: "When a self-pollinating species is invading a new habitat, a larger number of new lines might become established than in the case of a species population maintaining itself in the same habitat". These new lines may arise for two reasons. First, the secondary center may present a new order of diverse ecological sites to the species which then has the opportunity of generating genetic variation sufficiently rich enough to occupy these sites. Secondly, the natural (or human) selection constraints which suppressed variability in the primary center may not do so to the same extent in the secondary center and thus allow the species to expand and exploit the new ecological diversity. In either case, the genetic system of the species must be equal to the task. That is, it must be capable of generating and releasing variants into the heterogeneous environment. In the case of the Malawian bean populations this "capability" would, in part, consist of the existence of outcrossing. In addition, it must be reasoned that "off-types" are not selected out as they arise by the Malawian farmer. However, since the genetic expression of seed coat lags behind by one generation, it is doubtful whether a farmer could ever rid the population of recombinants.

The concept of a heterogeneous environment offering different "adaptive peaks" to a population was put forward by Wright (1931). He theorized that the structure which would best equip a population for continuous evolution in either a stable or an unstable environment would have three attributes. It would be:

1. A population of intermediate size, divided into subgroups, each separated spatially from each other but capable of occasional gene exchange.

2. Because of this exchange, the subgroups would share a common gene pool, and valuable new mutations could spread through the population.

3. Inbreeding within the subgroups, however, enables different subgroups to occupy slightly different "adaptive peaks".

Population stucture in Malawian bean landraces is analogous to this model. The landraces are usually of intermediate size (10 - 15,000 seeds). Although their subcomponents are not separated spatially, they are isolated by the prevalence of autogamy. However, this isolation is not complete due to occasional outcrossing. Thus, the subgroups (the individual lines in a mixture) do share a common gene pool and valuable new gene combinations may be generated and spread through the population. Finally, self-fertilization reproduces the new recombinations again and again over successive generations and endows the population with the potential to adapt to a wider array of environmental niches. Hence, the Malawian bean populations may provide a paradigm of Wright's optimal breeding structure.

Stebbins (1957) cites several characteristics of self-fertilizing species populations:

1. They consist of several morphological types each of which is represented by many similar or identical types.
2. These types can be recognized by distinctive characteristics so that the population appears like a cluster of closely related species.

3. In addition to these dominant types, there may exist several other recognizable types which are represented by only one or two individuals.
4. The dominant types breed true.
5. Occasionally, outcrossing occurs between biotypes resulting in vigorous F_1 hybrids.
6. In some species these hybrids are more vigorous than their parents; in others they are not.
7. These hybrids segregate, and the poorly adapted genotypes are eliminated.

These postulates were derived from the study of natural populations such as _Bromus carinatus_ (Harlan, 1945), _Senecio vulgaris_ (Haskell, 1953), and _Clarkia purpurea_ (Lewis & Lewis, 1955). Similar conclusions have been drawn from barley composite crosses, wild oats, and lima bean populations by Allard and his colleagues (Jain & Allard, 1960; Allard & Jain, 1962; Jain & Marshall, 1967; and Imam & Allard, 1965).

Jain and Allard (1960) discovered that the changes in genotypic frequencies occuring over 18 generations of a barley composite cross indicated that the decay in heterozygosity was much slower at several marker loci than that expected for the low level of outcrossing observed. This persistence of heterozygosis, they believe, is due in part to an advantage of the many new heterozygous combinations of genes available upon segregation from the initial hybrids, i.e. heterozygote superiority. They state

"This situation is in sharp contrast to that of experimental populations made up of mixtures of homozygous lines; there the number of "adaptive peaks" is small as shown by Harlan and Martini (1938) and the genetic potential of the population is limited". They conclude that the store of variability in a self-pollinating species is apparently not entirely associated with genetic diversity among multiple homozygous lines, since the storage potential of even a few superior heterozygotes could be substantial.

In subsequent work, Allard and Jain (1962) studied the quantitative genetic changes in the composite-cross of barley. They found that the population remained extremely variable even in the nineteenth generation. In addition, they discovered larger within family variances than in the homozygous parent lines. They suggest that "outcrossing at levels lower than those frequently observed in the so-called self-pollinating species can provide for high genetic variability in populations".

This population structure, however, was not encountered only in the rather artificial populations of the composite-crosses. Imam and Allard (1965) later documented the level of outcrossing and the variability in populations of wild oats (*Avena fatua*) in California - a predominantly self-pollinating species. Estimates of outcrossing, based on lemma color and rachilla pubescence, varied from one to twelve percent. They again found that the frequencies of genotypes for these monogenic traits indicated that a high reproductive advantage was associated with heterozygosity for the chromosome segments marked by these loci. Their measurements of genetic variability for days to flowering, plant height, number of tillers and seed number per panicle revealed a mosaic of highly localized differentiation. Considerable variation within each population existed and they suggest that ". . . a mixture of genotypes differing in morphology, physiological requirements and growth rhythyms may exploit the available moisture, light, and nutrients more efficiently than uniform populations where competition is between individuals of similar morphology and simultaneous requirements".

Kaplan (1981), in a recent paper, has raised the question of bean mixture advantage. He notes that varietal mixtures are seen in collections throughout the highland regions of Mesoamerica and Andean America, the postulated centers of origin of the common bean. While these mixtures appear to be less diverse than the Malawian mixtures, similar adaptive mechanisms may be at work. The bean mixtures which Kaplan has observed consist of four to six distinct types. Mixtures around Cajamarca, Peru collected by Zimmerer (1984, personal communication) consist of between 14 - 16 lines. Berlin, Breedlove and Raven (1974) have collected six different seed types within a single municipio in Chiapas, Mexico, but it is unclear if these were grown as mixtures by the local farmers. Kaplan (1981) states that a mixture dating over 1000 years B.P. (before present) has been excavated from an archaelogical site in the Mexico's Tehuacan valley. He claims its components are identical to contemporary market mixtures in the Tehuacan valley village of Ajalpan. If confirmed, this indicates that bean mixtures possess a unique intrapopulational balance which results in their persistence and stability over long periods of time.

Kaplan (1981) states that the "specific set of human and plant ecological factors which account for the existence and stability of mixed plantings is not clear". He found no nutritional advantage for rat growth as a result of feeding a mixture versus a single variety. He did, however, find evidence that the bean lines in a mixture germinate at different rates thereby extending the seedling establishment period. Such an extension would have obvious advantages if the first rains were interrupted. Kaplan also pointed out that mixtures in Latin America are confined to climbing beans. He reasoned this to be so because cultivators of climbing beans are used to harvesting over an extended period - climbing beans mature their pods over a two to three week period anyway. Cultivators of bush beans harvest their crop in a single operation. Thus a staggered ripening time due to differential emergence lends itself more to climbing genotypes. Interestingly, the majority of bean mixtures in Malawi also consists of climbing beans. Kaplan contends "Humans have originated not the components of mixtures but instead have assembled them from pre-existing variants into the mixtures that are adapted to particular production and land use systems. And, "Mixed planting may have been an idea that diffused from one area to another, but it need not have been so. The practice may be polyphyletic in origin . . ."

Whether the original beans introduced into Malawi were mixtures, or whether they were single lines later mixed by the Malawian farmers remains moot. What may be profitably investigated is the contemporary variability of these mixtures and the probable mechanisms by which this variability arises and persists.

Chapter 3

DIVERSITY IN MALAWIAN BEAN LANDRACES

Materials and Methods

Germplasm collection

The bean lines included in this study were collected in the northern region of Malawi between 25 February and 5 March, 1983 by a Bean/Cowpea C.R.S.P. team consisting of Leo Mapondo, Eric Ayeh and Greg Martin. This trip followed a preliminary collection effort in March 1982 by another Bean/Cowpea C.R.S.P. team consisting of Drs. M.W. Adams, O.T. Edje, P. Barnes-McConnell, D. Greenberg and Mr. Augustine Mkangama. Based on the observations of this earlier team, six areas were selected as being representative of the geographical, topographical and cultural diversity in the northern region. These areas, Chitipa North, Chitipa Central, Misuku Hills, Livingstonia Hills, South Rukuru Plain, and Mabulabo Traditional Authority were subsequently revisited. Five of these areas were chosen for the present study (Figure 4). Chitipa Central was excluded due to its proximity to Chitipa North and the desire to have an even distribution of geographical areas.

The 1983 team visited each area, contacted the local agricultural officers, and with their guidance collected

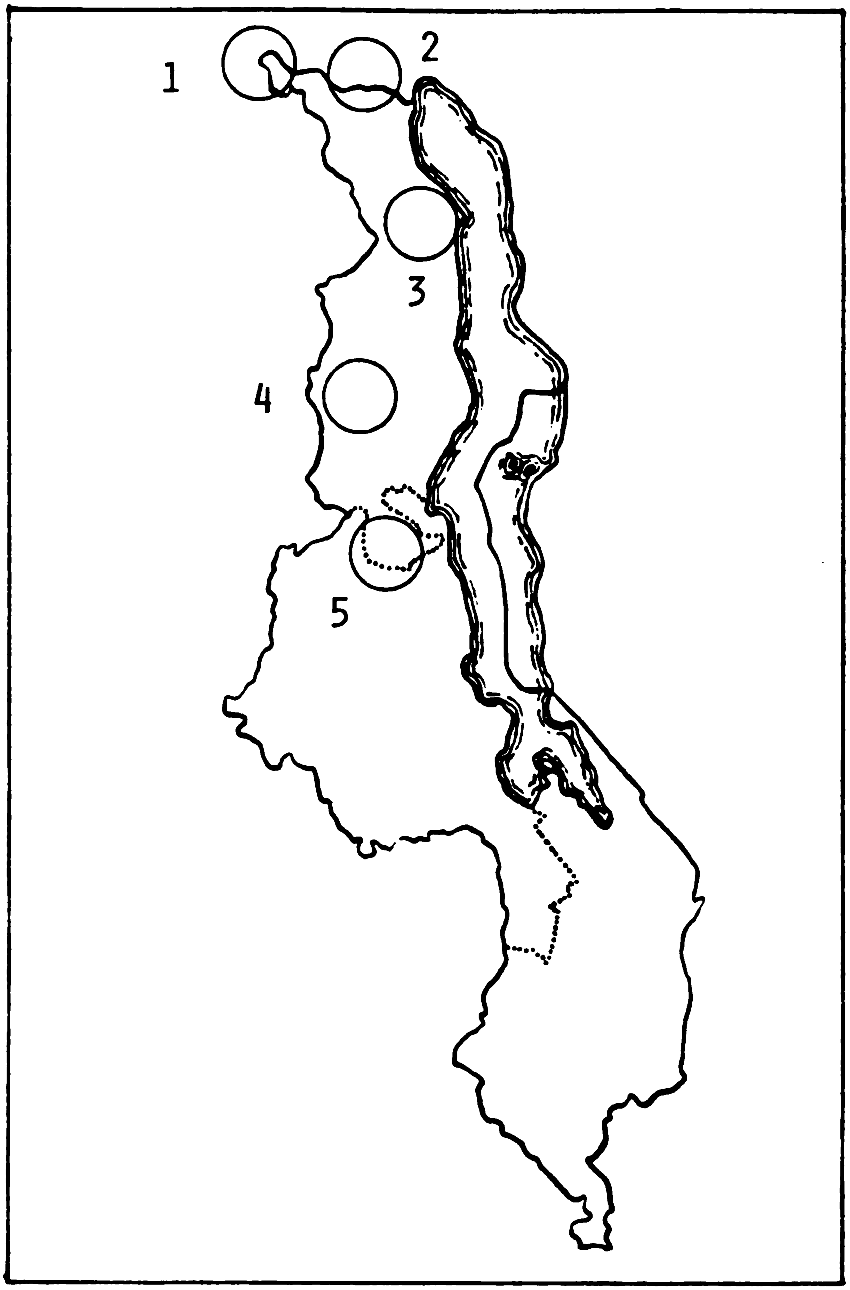
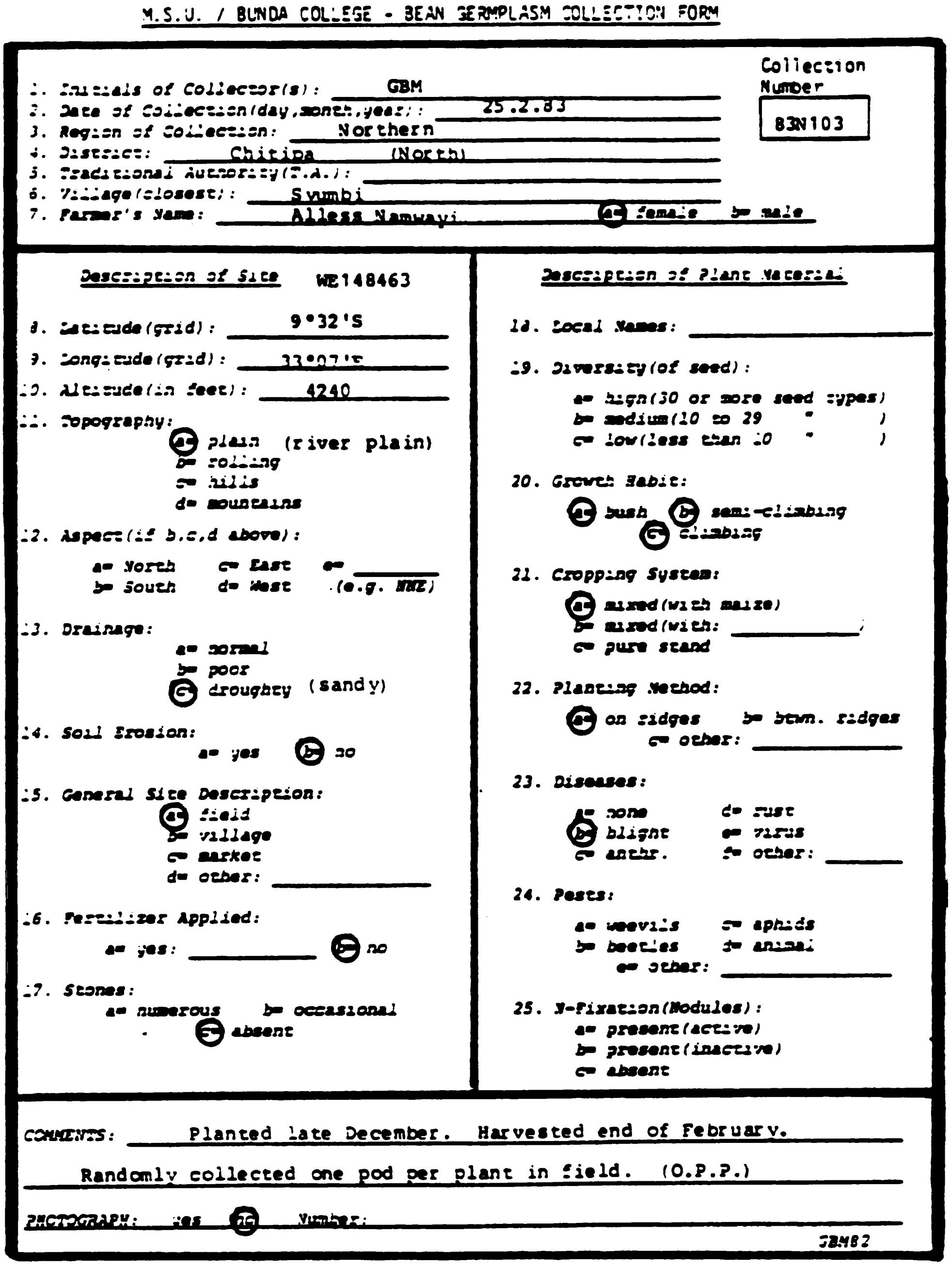


FIGURE 4: THE FIVE GEOGRAPHICAL AREAS FROM WHICH BEAN LANDRACES WERE COLLECTED.

1. CHITIPA NORTH
2. MISUKU HILLS
3. LIVINGSTONIA HILLS
4. SOUTH RUKURU PLAIN
5. MABULABO TRADITIONAL AUTHORITY

beans and supporting information from each of five farms. These farm sites were not selected with any particular criteria, but an attempt was made to sample sites which were evenly distributed throughout each area. The scenario of a typical visit was as follows. Through the interpretation of an agricultural officer, we would introduce ourselves and the purpose of the visit. Next, we would ask the farmer a series of questions about the village and her farming practices, especially those practices pertaining to bean landraces. This information, along with our own observations, was entered on a collection form (Figure 5). Special attention was given to obtaining accurate information on the location of the site so that , if required, it could be revisited. After these formalities, we asked if we could collect a sample of the farmer's beans. The Malawian farmers, without exception, responded with generosity and helpfulness at this point, allowing us to tramp through their fields, or if the beans had already been harvested, offering us beans from their storage pots. Thus, two distinct collecting methods were used. If the beans were still in the field, we would walk a transect across the field taking one pod from each plant that we passed. If the field was too small for this to yield a sufficient amount of seed (most were), then we would repeat this procedure leaving a few meters between the new transect and the old. The average sample size was 80 - 100 pods with this technique. Many farmers, especially as we proceeded



M.S.U. / BUNDA COLLEGE - BEAN GERMPLASM COLLECTION FORM

Collection Number: 83N103

1. Initials of Collector(s): GBM
2. Date of Collection(day,month,year): 25.2.83
3. Region of Collection: Northern
4. District: Chitipa (North)
5. Traditional Authority(T.A.): ______
6. Village(closest): Syumbi
7. Farmer's Name: Alless Namwayi [✓ a= female] b= male

Description of Site WE148463

8. Latitude(grid): 9°32'S
9. Longitude(grid): 33°07'E
10. Altitude(in feet): 4240
11. Topography:
    - [✓ a= plain] (river plain)
    - b= rolling
    - c= hills
    - d= mountains
12. Aspect(if b,c,d above):
    - a= North c= East e= ______
    - b= South d= West (e.g. NNE)
13. Drainage:
    - a= normal
    - b= poor
    - [✓ c= droughty] (sandy)
14. Soil Erosion: a= yes [✓ b= no]
15. General Site Description:
    - [✓ a= field]
    - b= village
    - c= market
    - d= other: ______
16. Fertilizer Applied: a= yes: ______ [✓ b= no]
17. Stones:
    - a= numerous b= occasional
    - [✓ c= absent]

Description of Plant Material

18. Local Names: ______
19. Diversity(of seed):
    - a= high(30 or more seed types)
    - b= medium(10 to 29 ")
    - c= low(less than 10 ")
20. Growth Habit: [✓ a= bush] [✓ b= semi-climbing] [✓ c= climbing]
21. Cropping System:
    - [✓ a= mixed(with maize)]
    - b= mixed(with: ______)
    - c= pure stand
22. Planting Method: [✓ a= on ridges] b= btwn. ridges c= other: ______
23. Diseases:
    - a= none d= rust
    - [✓ b= blight] e= virus
    - c= anthr. f= other: ______
24. Pests:
    - a= weevils c= aphids
    - b= beetles d= animal
    - e= other: ______
25. N-Fixation(Nodules):
    - a= present(active)
    - b= present(inactive)
    - c= absent

COMMENTS: Planted late December. Harvested end of February.
Randomly collected one pod per plant in field. (O.P.P.)

PHOTOGRAPH: yes [✓ no] Number: ______

GBM82

FIGURE 5: AN EXAMPLE OF A BEAN GERMPLASM COLLECTION FORM.

southwards, had already harvested their crop. In this case we would take several "random grabs" of seed from the sack or pot that was shown to us. With this technique we usually obtained 400 - 500 seeds. Both sampling strategies provided a random collection which, we felt, was representative of the farmer's landrace.

Before leaving the field a soil sample was collected, following the procedure recommended by Shickluna (1981). The soil was subsequently analysed at Bunda College of Agriculture for percentage of sand, silt and clay. Further analysis was carried out at Michigan State University for nitrate, potassium, phosphorous, pH, calcium, magnesium, zinc, manganese and organic matter.

Finally, an altitude reading, in meters, was taken at each site using a Thommen altimeter. The seed samples were then placed in cloth bags, labelled by farm site numbers, and returned to Bunda College of Agriculture.

Experimental Procedures

For this study, three of the five farm sites from each of the five geographical areas were selected (Figure 6). These fifteen sites were chosen by refering to the collection map and selecting sites which were evenly

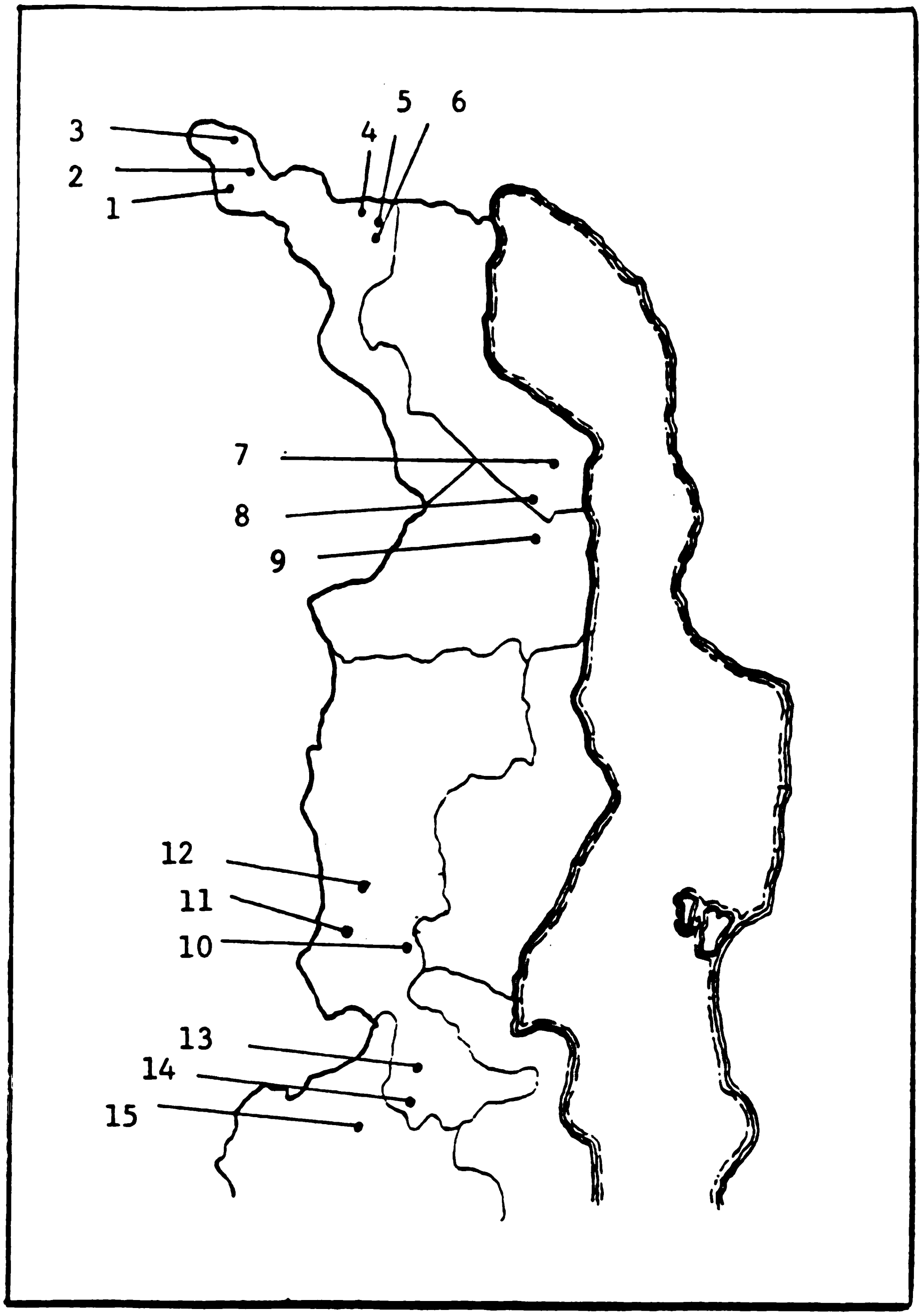


FIGURE 6: THE 15 COLLECTION SITES IN NORTHERN MALAWI.

1. Mweneloza village
2. Syumbi village
3. Ipenza village
4. Kasambra village
5. Kasumbi village
6. Kawotola village
7. Msuka village
8. Salawe village
9. Chaminono village
10. Chisusu village
11. Zebedea village
12. Kumwenda village
13. Chirwa village
14. Mafundeya village
15. Jengolima village

distributed within each area. No attention was given to the relative seed diversity of the particular collections. The fifteen sites are described and characterized in Tables 4 and 5. The results of the soil anaylsis for each site are given in Table 6.

It was decided, based on seed type variability, that 25 bean lines from each site would be sufficient to portray the landrace diversity and yet would still be manageable experimentally (Figure 7). Since 30 seeds were required of each of the 375 total lines, a seed increase was undertaken at Bunda College between 24 March and 10 July, 1983. A 66 seed random sample was taken from each of the 15 collections for this purpose. Two 33 seed plots for each site were established, with the seeds being sown randomly at 15 centimeter spacings in rows 90 centimeters apart. To minimize the chance of outcrossing in these plots the insecticide Sevin was applied every four days during flowering; no pollination activity was observed. At maturity, the first 25 plants in each site-plot were individually harvested and the seed was threshed, treated with Dieldrin and Thiram and placed into envelopes.

The 375 lines were grown at Bunda College of Agriculture between 26 July and 14 November, 1983 in a randomized complete block design with three replications. Also included in this study were four Michigan lines: Seafarer, Domino, Black Magic and Swan Valley. The maximum, minimum

Table 4: Names and locations of the 15 collection sites.

Area Village	Site No.	Altitude (meters)	Latitude	Longitude
Chitipa North		1288		
Mweneloza	1	1280	9°36'S	33°03'E
Syumbi	2	1292	9°32'S	33°07'E
Ipenza	3	1292	9°28'S	33°02'E
Misuku Hills		1560		
Kasambra	4	1494	9°39'S	33°33'E
Kasumbi	5	1609	9°42'S	33°34'E
Kawotola	6	1578	9°44'S	33°31'E
Livingstonia Hills		1159		
Msuka	7	1152	10°35'S	34°07'E
Salawe	8	1139	10°40'S	34°04'E
Chaminono	9	1188	10°46'S	34°02'E
South Rukuru Plain		1299		
Chisusu	10	1396	11°59'S	33°37'E
Zebedea	11	1292	11°56'S	33°27'E
Kumwenda	12	1210	11°52'S	33°23'E
Mabulabo T. A.		1276		
Chirwa	13	1402	12°21'S	33°34'E
Mafundeya	14	1219	12°34'S	33°37'E
Jengolima	15	1207	12°36'S	33°34'E

Table 5: Temperature, rainfall and daylength for the five collection areas*.

	Temperature** (Celsius)			Rainfall (millimeters)				Day-length***
Area	Low	High	$\bar{x}$	Dec.	Jan.	Feb.	$\bar{x}$	
Chitipa North	15.7	29.7	21.9	1790	2037	2189	2005	12h.37'
Misuku Hills	15.7	29.7	21.9	2940	2583	2571	2698	12h.38'
Livingstonia	15.7	30.0	20.8	2314	2556	2236	2368	12h.42'
South Rukuru	13.3	29.3	21.0	1875	2495	2026	2132	12h.45'
Mabulabo T.A.	13.3	29.3	21.0	1905	2465	2492	2287	12h.47'

* Source: National Meteorological Service, Chileka Airport, Blantyre, Malawi.

** Temperature figures are means for December, January and February.

*** Daylength is for 15 January, which would be the approximate date of flowering for beans planted in early December.

Table 6: Soil characteristics of the 15 collection sites.

Site No.	Sand %	Clay %	Silt %	pH	Phosphorous (lbs/acre)	Potassium (lbs/acre)	Calcium (lbs/acre)	Magnesium (lbs/acre)	Zinc (ppm)	Manganese (ppm)	Organic matter %	Nitrate (ppm)
1	68	13	19	5.7	24	185	1173	126	0.9	28.0	1.90	0.008
2	48	31	21	6.2	92	396	2600	480	3.6	38.0	3.60	0.012
3	78	9	13	6.4	136	244	1387	216	3.6	35.0	2.24	0.017
4	11	62	27	5.5	24	379	1387	149	0.9	48.6	4.50	0.210
5	45	40	15	7.0	201	729	4267	514	7.3	62.2	5.40	0.174
6	48	34	18	5.9	15	362	1700	320	0.9	47.6	5.52	0.375
7	22	40	38	5.6	11	488	1900	514	1.8	35.0	3.67	0.454
8	38	36	26	5.9	105	738	1387	370	1.8	53.3	4.95	0.174
9	58	16	26	5.7	98	354	1387	273	1.8	15.5	4.29	0.413
10	80	10	10	6.1	75	111	640	69	0.9	18.2	1.79	0.158
11	74	20	6	5.8	141	185	747	80	0.9	31.0	2.62	0.281
12	80	10	10	6.1	145	168	747	103	0.9	18.2	2.26	0.309
13	56	31	13	6.0	39	362	1387	198	3.6	39.0	3.22	0.606
14	80	10	10	5.8	189	111	640	57	0.9	20.0	2.17	0.211
15	80	6	14	7.7	172	111	2400	216	0.9	47.6	3.83	0.454
CA*	58	24	18	6.1	98	328	1583	246	2.0	35.8	3.46	0.257
MA**	59	17	24	5.4	70	405	n/a	n/a	n/a	n/a	2.24	n/a

* Average for collection sites

** Average for Malawi. (Sillanapa, M., 1982).

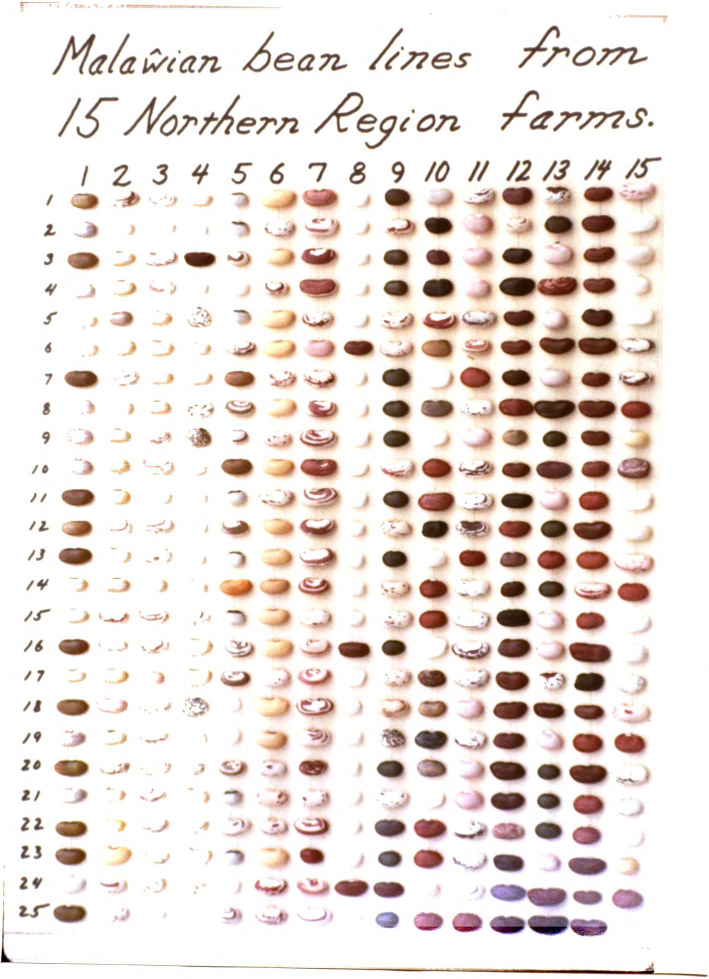
Figure 7

Seed types of the 375 bean lines included in the study.

Note:

1. Each column constitutes the 25 lines collected from the farm site indicated at the top of the chart.

2. Two mistakes were made in mounting the seeds to the board. Lines 16 and 17 from site 3 should be reversed. Lines 11 and 12 from site 5 should also be reversed.


Malaŵian bean lines from
15 Northern Region farms.
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22
23
24
25

and mean air temperatures in degrees Celsius during the the egrowing season were: July - 23.7, 11.1, 14.8; August - 24.8, 11.1, 15.3; September - 28.9, 14.1, 20.2; October - 29.9, 15.5, 22.2; November - 31.6, 18.2, 24.4. Total rainfall over the growing season was 10.6 millimeters.

The seeds of each line were sown 10 centimeters apart, with 10 seeds per plot, in rows 10 meters long and 90 centimeters apart. Thus, each row contained 8 plots and a block consisted of 50 ten-meter rows. Germination was greater than 95% in the field overall. Three weeks after planting, in the process of taking hypocotyl length and seedling dry weight measurements, the plots were thinned to six plants. Thinning was accomplished by removing the first, fourth, seventh, and tenth plant from each plot. This left three groups of two plants each, the two plants being separated by 10 centimeters and the two-plant pairs being separated by 20 centimeters. A pole was then placed between each two-plant pair. Coupled with the 90 centimeter row spacing, this planting arrangement minimized competition between plants and lessened the number of poles required for staking.

Standard bean cultural methods as practiced at Bunda College of Agriculture were followed throughout this study. Each 10 meter ridge was fertilized with 273 grams (300 kg/ha) of 20-20-0, N-P-K. The plots were furrow irrigated (one or two blocks at a time) whenever required - usually once a week. Leafhoppers were controlled with alternate applications of Sevin and Lebicyd. Diseases were not a problem since this was the dry season, however, Plantvax was sprayed late in the season to control a slight rust infestation. The plots were kept entirely weed-free. Four weeks after planting, and occasionally throughout the season, the ridges were "rebanked" to aid in supporting the plants. The plots were harvested one block at a time beginning on 31 October and continuing until 14 November, 1983.

Character measurements and scores

Measurements and scores were recorded for each line during the growing season. The recording was done one block at a time to minimize within block variation. An attempt was made to choose characters which would portray a broad picture of the architecture of the germplasm. Detailed descriptions and comments for each character follow. Summaries of the quantitative and qualitative characters are given in Table 7.

Phenological characters

1. Days to emergence

Days were counted from the date of first irrigation (27 July for replications 1 and 2, 28 July for replication 3) to

Table 7: Character codes and summary of quantitative and qualitative character measurements.

Code	Character	Experimental unit	Scale
Phenological characters			
P1	Days to emergence	plot	number
P2	Days to first flower	"	"
P3	Days to end of flowering	"	"
P4	Flowering duration	"	"
P5	Days to physiolog. maturity	"	"
Morphological characters			
M1	Leaflet area	3 plants	centimeters^2
M2	Leaflet length	"	"
M3	Leaflet width	"	"
M4	Leaflet shape	"	length / width
M5	Petiole length	"	centimeters
M6	Hypocotyl length	1 - 3 plants	centimeters
M7	Seedling dry weight	"	grams
M8	Hypocotyl diameter	3 plants	1/32 inch
M9	Nodes on main stem	2 - 3 plants	number
M10	Seed length	1 seed	centimeters
M11	Seed width	"	"
Agronomic characters			
A1	Single seed weight	100 seeds	grams
A2	Seeds per pod	15 pods	number
A3	Pods per plant	plot	"
A4	Seed yield	plot/#plants	grams
A5	Seeds per plant	"	"
Qualitative characters			
Q1	Hypocotyl color	plot	1,2,3 *
Q2	Standard color	"	1,2,3,4,5
Q3	Wing color	"	"
Q4	Seed primary color	1 seed	1 - 15
Q5	Growth habit	plot	0,1

* See text for explanation of qualitative scales.

the date when at least 5 of the 10 seedlings had emerged and their primary leaves had unfolded.

2. Days to first flowering

This was scored on a plot basis. The days were counted from the date of first irrigation up until at least 50% of the plants had opened at least one flower. Data were taken every other day.

3. Days to end of flowering

Recorded on a plot basis. When 50% or more of the plants had finished flowering the number of days from first irrigation was recorded. The type 1 beans could be easily scored for this character. The indeterminate lines presented greater difficulty as these were occasionally still flowering at harvest. For these, an arbitrary criterion was set. When flowering had ceased below the tenth node, this date was recorded as end of flowering. For a type 4b this may be misleading, but as a whole it should accurately indicate differences among lines.

4. Duration of flowering

The difference between days to end of flowering and days to first flower was calculated.

5. Days to physiological maturity

This was recorded on a plot basis, the interval being figured from the first day of irrigation to that when 90% of the pods had turned yellow or to an intermediate color (e.g. purple).

Morphological characters

6. Leaflet area (cm.^{2})

Leaflet area, in centimeters squared, was measured using a Li-Cor portable leaf area meter, model LI-3000. The measurements were taken when the third trifoliate had unrolled on 90% of the plants in the field. The measurements were taken on the first trifoliate leaf, the terminal leaflet. In most cases, the first three plants encountered in each plot were the one's measured. However, if one (or two) of these plants were diseased, stunted or otherwise grossly abnormal, the next normal plant was chosen. Three plants were measured for each entry in each replication. After measuring, a hole was made in the leaflet with a paper punch.

7. and 8. Leaflet length and width (cm.)

Using the punched hole as identification, these measurements were taken on the same leaflet as the leaf area. The length of the leaflet was measured from the point where the pedicel joins the leaflet to the tip. The width was measured at the widest point.

9. Leaflet shape

Leaf shape in general is deltoid, but considerable variation may be observed from long, narrow leaflets to short, broad leaflets. The ratio of length/width was calculated to portray this variation.

10. Petiole length (cm.)

This measurement was taken on the same leaflet as the leaflet measurments. The petiole length was taken from the leaflet base to the abscission line.

11. Hypocotyl length (cm.)

Hypocotyl length was recorded on three plants removed during thinning. In general, these were the first, fourth, and seventh seedlings. The length was recorded from the end of the hypocotyl to the cotyledonary scar.

12. Seedling dry weight at four weeks (gms.)

The three plants which were used for the hypocotyl length measurments were then taken, their roots rinsed in water to remove excess soil, and placed in paper bags. These were then placed in a drying oven at 110 ^{o}C for 24 hours. The dried weight of all three seedlings was then recorded, and the average weight per seedling was calculated.

13. Hypocotyl diameter (1/32 inch)

This measurement was taken on the first three plants in each plot, just before flowering. A pair of calipers, with increments of 1/32 inch was used, although readings were taken to 1/64 inch. The calipers were placed one centimeter below the cotyledonary scar. The number was entered as 1/32 inch, thus 8.5, for example, is actually 17/64 inch.

14. Node number on main stem at physiological maturity

This was recorded in replication 1 only. Two plants per plot were counted for indeterminate types, three plants per plot for determinate types.

15. and 16. Seed length and seed width (cm.)

Seed length and width were recorded for one random-normal seed per entry.

Agronomic characters

17. Single seed weight (gms.)

Seed weight was calculated from a 100-seed sample of each line. The fresh seeds were first weighed, then oven-dried at 110 °C for 48 hours, then weighed again. Seed weight was adjusted to 10% moisture.

18. Seeds per pod

This was calculated from a 25-pod sample from each plot.

19. Pods per plant

This was calculated from the total seed yield, the single seed weight, and the number of seeds per pod.

20. Yield per plant (gms.)

Seed yield per plant was calculated from the seed yield per plot divided by the number of plants per plot, and adjusted to 10% moisture.

21. Seeds per plant

Fecundity was calculated by dividing adjusted yield by the adjusted single seed weight.

Qualitative characters

22. Seed primary color

Seed color was scored using a modification of the classification scheme in *Descriptors for Phaseolus vulgaris L.* (Anon., 1982).

1. Black
2. Brown
3. Maroon
4. Grey
5. Yellow
6. Cream/Buff
7. Pure white
8. Whitish
9. White with purple tinge
10. Blue
11. Green
12. Red
13. Pink
14. Purple
15. Other

These color categories were considered to encompass a range of hue. A descriptor chart, with examples of the range of colors "permitted" under each category, was used as an objective criterion (Figure 8). Thus, 'yellow' ranges from pale yellow, bright yellow, to a sort of greenish-yellow. Likewise 'brown' encompassed everything from light brown to sepia. A distinction was made between 'red' and 'maroon', both common colors and easily distinguished in the Malawian germplasm. The standard for 'white' was Seafarer, the standard for 'whitish' was Swan Valley. Considering the complexity of seedcoat color genetics in _P. vulgaris L._, this latitude in color categories probably disallows a specific color-to-genotype correspondence. Still, the beans within one category, though varying in hue, likely have some genes in common.

23. _Banner color_

The banner (or standard) color of each line was scored when the 'days to first flower' was recorded. This was taken on a plot basis and only for replication 1. An arbitrary scale was followed:

1. White
2. Greenish-white
3. Pink
4. Lilac
5. Purple

There was little ambiguity using this scale. Flower color was always scored early in the morning to avoid mistakes due to fading or darkening.

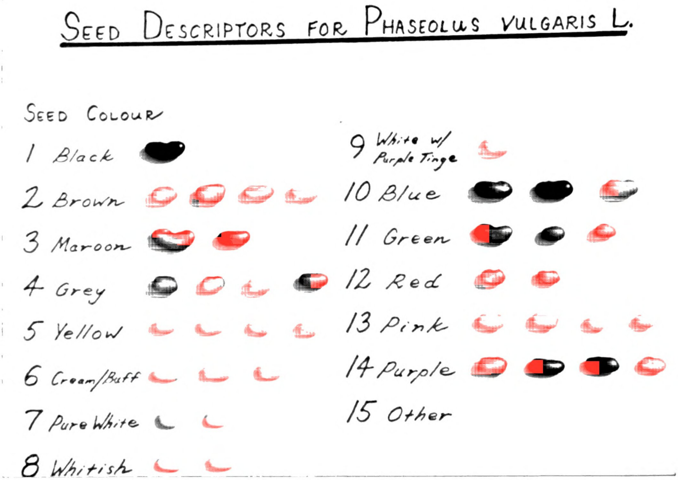

Figure 8: The seed color 'descriptor chart'.

24. Wing color

It was decided to take wing color along with banner color since the two are rarely the same. The same 1 - 5 scale was used.

25. Hypocotyl color

Hypocotyl color was scored using an arbitrary scale:

1. Green
2. Pink
3. Purple

26. Growth habit

This was actually a score for determinancy (score = 1) versus indeterminancy (score = 2). It was decided not to score for specific growth types (e.g. types 1,2,3,4) since the staking and "training" made it difficult to consistently differentiate between types 3 and 4.

27. Segregation

Several lines were observed to be segregating for hypocotyl color, flower color, and growth habit during the course of the study. At harvest several more were seen to be segregating for seed color, pattern and size. Segregation for each character was recorded in the data book. Samples of some of the seed types which segregated from some of the lines were saved and used in constructing seed charts depicting probable recombinational events at representative farms.

Data Analysis

A) Variation of the bean landraces

The objective of this section of the analysis was to provide a quantitative description of the variability between areas, between sites within areas, and between lines within sites.

The frequency of each character state (e.g. green, pink, purple hypocotyl) for the qualitative traits was calculated for each site. Histograms were constructed to depict the area-to-area variation across the northern region.

Means for the 21 quantitative variables were calculated for the northern region as a whole, the five geographical areas, and the 15 sites.

Separate analyses of variance for the 18 replicated character measurements were performed to test for significant differences between areas, between sites within areas, and between lines within sites. Least significant differences (LSD) were calculated for those characters having significant differences between areas and between sites within areas. Those traits which were statistically significant were used in a principal components analysis (PCA).

A modification of a PCA program contained in the Genstat Package of Statistical Programs, Rothamstead Agricultural Experimental Station, was used to calculate distances between areas and between sites within areas. This modified program, originally used to calculate distances between a sample of U.S. bean cultivars by Dr. M.W. Adams (1977), is described in more detail in a later report (Adams & Wiersma, 1978). The program results in principal component scores (PC's) based on standardized data. These scores are normalized, and then used in calculating the distances between taxonomic units. It was decided to calculate all distances based on the first six PC's after preliminary trials indicated that these accounted for greater than 95% of the variance. Area means and site means were used to calculate the distances. Since several phenological traits were statistically significant between areas in the analyses of variance, the five phenological characters were also run in a separate principal component analysis.

Finally, to illustrate the similarities and dissimilarities between individual areas and sites, the 'Scatter' procedure in the Clustan Cluster Analysis Package was used to plot the standardized scores for PC's I and II.

B) Environmental / Plant character associations

Correlations between 8 site variables: altitude, latitude, sand %, pH, phosphorous, potassium, nitrate, "heterozygosity level" (the percentage of lines segregating from each farm) and the 21 quantitative traits were calculated.

C) Population structure in the landraces

In order to elucidate populational structure, further analyses were performed on the 15 individual landraces.

The 25 line means (over replications) from each collection were used in 15 separate analyses using the Genstat PCA program. The maximum and minimum distances between two-line pairs from each site were tabulated. Since the pedigree relationships are known between the four Michigan lines included in the study, their distances were calculated and used in comparing the probable genetic relationship between certain lines in the landraces.

Several site-collections consisted of two to four homogenous seed types which, it was felt, may actually be identical by descent, i.e. pure lines. Two of these sites, site 1, Mweneloza village (containing 3 major seed types) and site 6, Kawotola village (containing 2 seed types) were analysed further to test for statistically significant differences within these uniform seed types. Analyses of variance for the 18 continous variables were performed on brown, purple-speckled, and yellow seeded types from site 1, and on tan/red mottled and yellow seeded types from site 6. The average distances between lines within each of these types was calculated.

Principal component scores on the first six components for six lines in the brown seeded group from site 1 were compared to provide further information on the similarities or dissimilarities between these lines.

Finally, using the "Scatter" procedure in Clustan, each site-collection was plotted separately on PC's I and II to portray the diversity pattern within the landrace. These plots were used to hypothesize about recombinational events which may have occured to give rise to the rare seed types observed in many landraces.

Chapter 4

DIVERSITY IN MALAWIAN BEAN LANDRACES

Results

A) Variability in the landraces.

The most striking indication of variability in the Malawian bean landraces is the diversity of seed colors, patterns, shapes and sizes (Figure 7). There is a marked transition in seed types as one proceeds from north to south in the northern region. The Chitipa North and Misuku Hills areas, in general, are characterized by landraces consisting of brown, yellow and tan/red mottled beans. The two southernmost areas, South Rukuru Plain and Mabulabo contain mostly red and other solid-colored beans. No oblong yellow beans are observed south of the Misuku Hills in these collections, and no solid red beans are observed north of the Livingstonia Hills. This sharp demarcation is not seen in the tan/red mottled beans which are common and are distributed throughout the northern region. The Livingstonia Hills area (sites 7, 8, 9), while geographically the central area in this study, is characterized by several anomolous mixtures. Site 7 is the only collection which has zebra-striped beans comprising the majority of the landrace. Site 8 appears to be a simple mechanical mixture and is the only site having white beans as a predominant component. Site 9 contains a large proportion of an olive-green bean known as "Nyauzembe". This type is common around Rumphi but is rare elsewhere, although it did appear at site 13 as a minor component. Many of the common seed types have been named by the local tribes. Endemic types are often known by a single name (e.g. Nyauzembe, see site 9, line 7) and may be examples of established "primitive varieties". Other more cosmopolitan types are recognized by several tribes and correspondingly have many names (e.g. Mwikala (in Ndali); Musiska (in Lambya); and Chibamba (in Chichewa) all refer to a red, oblong seed type, see site 14, line 4). Most landraces consist of 4 - 8 different seed types. Some landraces, for example, those from sites 10 and 12, contain far more. A few mixtures contain only two seed types. Seed type alone, however, is not an indication of the level of variability in a landrace. Considerable variability for other plant characteristics may exist within a seemingly homogeneous seed type. Many landraces contain seeds which appear to be "off-types". In many cases these unusual types were found to be segregating, thus indicating that they were in fact recombinant types. Farm sites 10 and 12 were most notable in this respect.

Banner and wing color frequencies vary widely between sites within areas and between areas (Table 8). Lilac and purple are the most common banner colors, and pink is the most common wing color. The five banner colors were

Table 8: Banner and wing color frequencies in the 15 landraces.

Site	Banner					Wing				
	1	2	3	4	5	1	2	3	4	5
1	28.0	-	68.0	4.0	28.0	-	68.0	4.0	-	-
2	-	4.0	-	68.0	28.0	4.0	-	96.0	-	-
3	-	12.0	-	20.0	68.0	12.0	-	88.0	-	-
Area Mean	-	14.7	-	52.0	33.3	14.7	-	84.0	1.3	-
4	32.0	-	16.0	36.0	16.0	48.0	-	44.0	8.0	-
5	16.0	4.0	-	44.0	36.0	20.0	-	44.0	4.0	32.0
6	-	-	-	68.0	32.0	-	-	92.0	8.0	-
Area Mean	16.0	1.3	5.3	49.3	28.0	22.7	-	60.0	6.7	10.7
7	-	8.0	-	68.0	24.0	8.0	-	92.0	-	-
8	88.0	-	-	8.0	4.0	88.0	-	8.0	4.0	-
9	-	-	56.0	4.0	40.0	56.0	-	44.0	-	-
Area Mean	29.3	2.7	18.7	26.7	22.7	50.7	-	48.0	1.3	-
10	8.0	12.0	12.0	44.0	24.0	20.0	4.0	36.0	40.0	-
11	-	-	-	44.0	56.0	-	-	44.0	56.0	-
12	-	8.0	12.0	8.0	72.0	-	16.0	8.0	76.0	-
Area mean	2.7	6.7	8.0	32.0	50.7	6.7	6.7	29.3	60.7	-
13	-	4.0	28.0	60.0	8.0	28.0	-	64.0	8.0	-
14	-	-	12.0	40.0	48.0	4.0	8.0	44.0	44.0	-
15	8.0	16.0	32.0	20.0	24.0	36.0	4.0	40.0	16.0	4.0
Area Mean	2.7	6.7	24.0	40.0	26.7	22.7	4.0	49.3	22.7	1.3
Region Mean	10.1	6.4	11.2	40.0	32.3	23.5	2.1	54.1	17.9	2.4

observed in all areas except area 1, where no white or pink banners were found. Only the Mabulabo area had all of the wing colors present, the other areas lacked one or more. Although considerable variability between areas was observed for flower color, no clinal pattern is evident (Figures 9 and 10).

All of the populations were polymorphic for hypocotyl color (Table 9). In all but area 1 each color state was observed with greater than 10% frequency (Figure 11).

Indeterminate beans were observed in every landrace (Table 9). All but three landraces also contained at least one determinate line. Overall, indeterminate beans predominate in the northern region (Figure 12). However, individual landraces may contain large proportions of determinate types (e.g. sites 6 and 7).

Table 10 presents the mean values and ranges for the 21 quantitative characters measured in the study. A considerable range for all characters is evident and is indicative of appreciable variability in the northern region.

The analyses of variance for the 18 replicated character measurements revealed statistically significant differences between areas for three phenological characters, days to

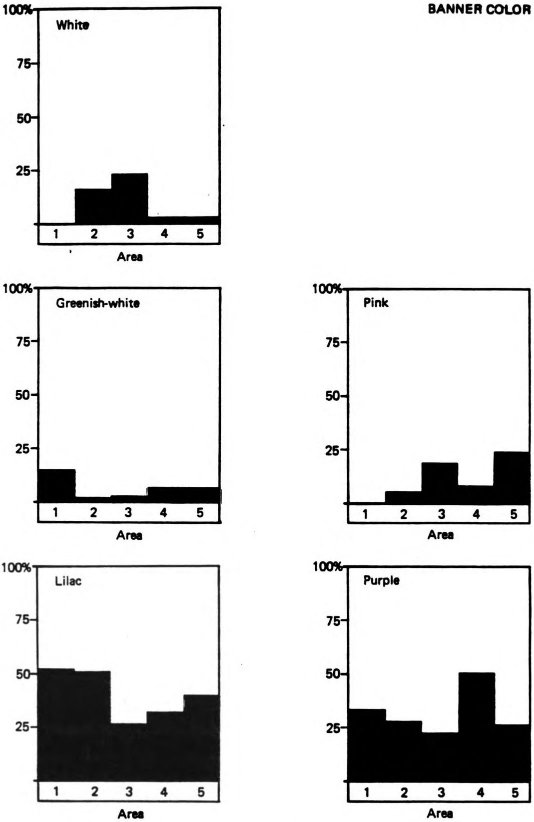

FIGURE 9: Frequencies of the banner colors for the 5 geographical areas in the northern region of Malawi.

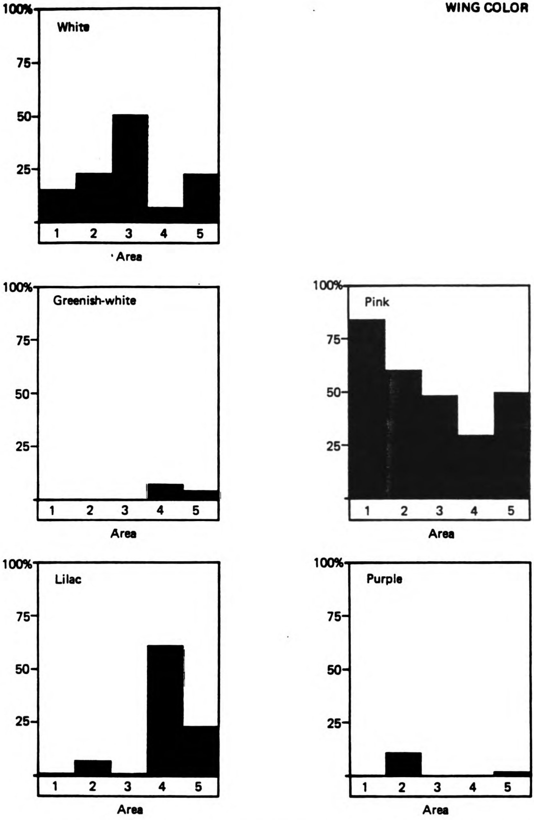

FIGURE 10: Frequencies of the wing colors for the 5 geographical areas in the northern region of Malawi.

Table 9: Growth habit and hypocotyl color frequencies in the 15 landraces.

Site	Growth habit		Hypocotyl color		
	1	2	1	2	3
1	-	100.0	36.0	60.0	4.0
2	4.0	96.0	44.0	56.0	-
3	8.0	92.0	72.0	24.0	4.0
Area Mean	4.0	96.0	50.7	46.7	2.7
4	32.0	68.0	52.0	28.0	20.0
5	4.0	96.0	20.0	40.0	40.0
6	92.0	8.0	32.0	60.0	8.0
Area Mean	42.7	57.3	34.7	42.7	22.7
7	96.0	4.0	20.0	72.0	8.0
8	8.0	92.0	88.0	8.0	4.0
9	40.0	60.0	36.0	44.0	20.0
Area Mean	48.0	52.0	48.0	41.3	10.7
10	4.0	96.0	20.0	28.0	52.0
11	4.0	96.0	4.0	44.0	52.0
12	-	100.0	8.0	12.0	80.0
Area Mean	2.7	97.3	10.7	28.0	61.3
13	4.0	96.0	4.0	84.0	12.0
14	28.0	72.0	-	48.0	52.0
15	-	100.0	40.0	48.0	12.0
Area Mean	10.7	89.3	14.7	60.0	25.3
Region Mean	21.6	78.4	31.7	43.7	24.6

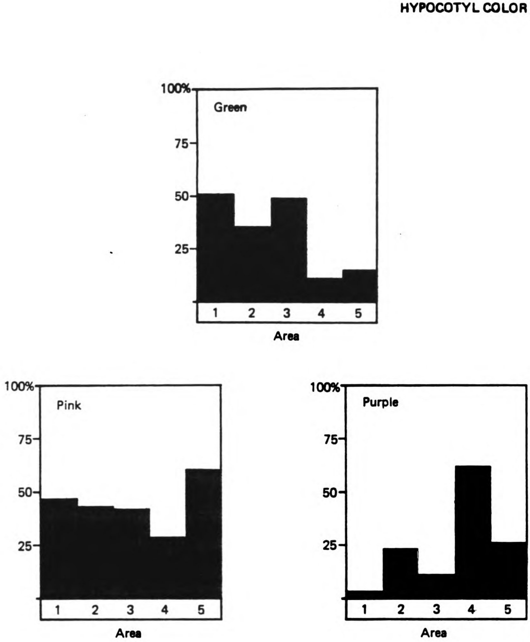

FIGURE 11: Frequencies of the hypocotyl colors from the 5 geographical areas in the northern region of Malawi.

GROWTH HABIT

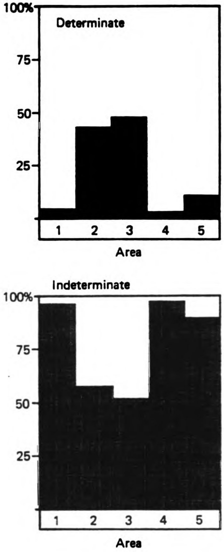

FIGURE 12: Frequencies of determinate and indeterminate growth habits from the 5 geographical areas in the northern region of Malawi.

Table 10: Mean values and ranges for the 21 quantitative variables for the northern region of Malawi.

Character	Mean	Range
Days to emergence	12.82	10 - 21
Days to first flower	51.07	44 - 65
Days to end of flowering	70.00	61 - 84
Duration of flowering	18.93	5 - 32
Days to physiol. maturity	96.88	84 - 118
Leaflet area ($cm.^2$)	46.49	10.4 - 81.1
Leaflet length (cm.)	10.43	5.2 - 14.7
Leaflet width (cm.)	6.85	3.3 - 9.9
Leaflet shape	1.54	0.7 - 2.9
Petiole length (cm.)	5.64	1.7 - 9.3
Hypocotyl length (cm.)	6.79	3.7 - 9.9
Seedling dry weight (gms.)	1.82	0.2 - 4.0
Hypocotyl diameter (1/32")	8.16	5.3 - 10.7
Nodes on main stem	16.42	4.7 - 31.0
Seed length (cm.)	1.47	0.8 - 2.0
Seed width (cm.)	0.76	0.5 - 0.9
Single seed weight (gms.)	0.43	0.12 - 0.68
Seeds per pod	4.49	1.93 - 7.07
Pods per plant	32.29	2.52 - 99.90
Seed yield per plant (gms.)	58.60	2.51 - 162.52
Seeds per plant	146.80	8.60 - 479.70

first flower, duration of flowering, and days to physiological maturity (Table 11). The mean differences between collection areas are presented in Table 12. Statistically significant differences between sites within areas were observed for all characters at the 0.01 probability level (Table 13).

The first two principal components (PC's) from the analysis of area means for the 21 quantitative characters accounted for 83.48% of the variance (Figure 13). Based upon these two PC's, areas 2 and 3 appeared to contain very similar landraces. The other three areas are widely dispersed on the plot and indicate a considerable dissimilarity, in general, between areas. The distances between areas based on the scores of the first six standardized and normalized PC's are presented in Table 14 and graphically in Figure 16. These distances reveal a different, but perhaps more accurate picture of the relationships between areas. Areas 2 and 5 share the greatest similarity, while areas 3 and 4 are the most dissimilar. These two portrayals of inter-area variability, while not agreeing in specific relationships, nevertheless demonstrate that geographical proximity of two areas does not necessarily result in a close relationship when the areas' landraces are viewed multivariately. Thus, for example, areas 1,2 and areas 4,5 share many similar seed types and are geographically close but according to this

Table 11: Analysis of variance for the 18 replicated character measurements.

Character code ++		Mean squares			
		Areas	Sites	Lines	Error
	Df	4	10	360	748
P1		9.85	10.60**	3.36**	1.52
P2		2420.50**	246.50**	18.98**	2.70
P3		3048.25**	1038.80**	33.63**	4.18
P4		1518.76	381.70**	21.62**	5.10
P5		3711.92**	407.50**	32.11**	8.51
M1		123.63	2408.52**	163.87**	84.50
M2		28.01	47.72**	2.75**	1.26
M3		3.06	15.57**	1.27**	0.74
M4		0.37	0.22**	0.05**	0.02
M5		15.43	8.93**	1.18**	0.48
M6		10.92	4.63**	1.02**	0.59
M7		1.20	2.75**	0.21**	0.10
M8		14.14	12.46**	0.92**	0.42
A1		0.32	0.39**	0.19**	0.01
A2		4.39	11.96**	0.83**	0.12
A3		3665.06	5166.53**	227.85**	66.54
A4		14972.20	4556.50**	525.39**	230.49
A5		58194.56	192942.34**	6616.25**	1431.32

** Significantly different at the 0.01 probability level.

++ See table 7 for description of character codes.

Table 12: Mean differences between collection areas for 21 quantitative characters.

Character	Area					LSD (P = .01)
	1	2	3	4	5	
Days to emergence	12.71	12.70	12.81	13.19	12.70	
Days to first flower**	46.31	50.15	50.61	54.64	53.63	3.63
Days to end of flowering	68.62	67.20	66.79	75.56	71.82	
Duration of flowering**	22.31	17.06	16.18	20.92	18.19	4.52
Days to P. M.**	92.77	93.42	97.00	102.77	98.45	4.67
Leaflet area (cm.^{2})	46.98	44.49	44.31	46.55	50.08	
Leaflet length (cm.)	10.53	10.10	10.10	10.44	10.96	
Leaflet width (cm.)	6.74	6.79	6.73	6.98	6.99	
Leaflet shape	1.58	1.49	1.50	1.51	1.58	
Petiole length (cm.)	5.81	5.18	5.68	5.75	5.79	
Hypocotyl length (cm.)	7.03	6.53	6.58	6.87	6.93	
Seedling dry weight (gms.)	1.16	1.10	1.16	1.20	1.30	
Hypocotyl diameter (1/32")	7.96	8.05	7.98	8.20	8.57	
Nodes on main stem	17.73	13.93	11.80	21.23	17.43	
Seed length (cm.)	1.51	1.38	1.41	1.54	1.52	
Seed width (cm.)	0.74	0.73	0.75	0.79	0.77	
Single seed weight (gms.)	0.45	0.40	0.39	0.45	0.48	
Seeds per pod	4.45	4.59	4.66	4.30	4.45	
Pods per plant	28.27	32.89	31.33	38.85	30.11	
Seed yield / plant (gms.)	55.91	54.30	49.59	70.57	62.62	
Seeds per plant	126.30	154.12	154.43	165.12	133.87	

** Significantly different for this character at 0.01 probability level.

Table 13: Mean differences between collection sites for 21 quantitative characters.

Character code ++	Site															LSD* (P = 0.01)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
P1	12.48	12.68	12.96	12.91	12.39	12.81	13.48	12.43	12.53	13.71	12.88	12.97	12.84	12.52	12.75	0.77
P2	46.33	45.96	46.63	50.33	53.21	46.89	49.24	52.84	49.76	55.84	54.12	53.96	53.75	52.37	54.76	1.84
P3	69.13	68.04	68.68	68.16	71.65	61.80	61.61	73.84	64.92	76.41	74.00	76.25	70.92	71.01	73.52	2.44
P4	22.76	22.04	22.08	17.84	18.36	14.84	12.40	21.04	15.24	20.60	19.84	22.36	17.16	18.52	18.80	1.96
P5	93.91	91.56	92.85	93.93	96.29	90.05	98.36	99.44	93.20	104.84	100.83	102.64	97.64	98.40	99.32	2.39
M1	46.37	46.05	48.37	41.46	42.78	49.24	53.03	32.30	47.58	42.10	49.38	48.19	50.15	46.79	53.42	5.39
M2	10.57	10.44	10.59	9.62	9.99	10.69	11.39	8.41	10.52	10.01	10.77	10.53	11.26	10.26	11.35	0.70
M3	6.78	6.51	6.93	6.61	6.61	7.16	7.42	5.80	6.98	6.62	7.13	7.18	6.72	6.94	7.30	0.48
M4	1.56	1.62	1.54	1.46	1.52	1.51	1.54	1.46	1.51	1.54	1.53	1.48	1.68	1.49	1.56	0.09
M5	6.14	5.45	5.83	5.14	5.19	5.22	5.74	5.38	5.91	5.33	6.08	5.85	5.83	5.26	6.27	0.46
M6	7.14	6.94	7.01	6.42	6.65	6.52	6.69	6.03	7.02	6.86	6.73	7.02	6.81	6.96	7.02	0.43
M7	1.18	1.13	1.18	0.96	1.02	1.32	1.33	0.79	1.35	1.06	1.40	1.16	1.28	1.18	1.42	0.19
M8	8.04	7.92	7.92	7.93	7.63	8.59	8.41	7.28	8.24	7.90	8.65	8.05	8.38	8.48	8.84	0.40
M9	19.30	16.00	17.90	15.00	20.00	6.80	7.00	16.60	11.80	23.00	18.20	22.50	16.50	15.20	20.60	+
M10	1.52	1.48	1.52	1.32	1.23	1.58	1.69	1.05	1.48	1.47	1.62	1.52	1.46	1.54	1.56	+
M11	0.75	0.72	0.76	0.74	0.70	0.75	0.79	0.67	0.78	0.79	0.80	0.77	0.77	0.76	0.79	+
A1	0.48	0.43	0.44	0.38	0.36	0.46	0.49	0.24	0.42	0.40	0.53	0.41	0.49	0.44	0.49	0.06
A2	4.21	4.49	4.66	4.49	4.87	4.42	4.13	5.59	4.26	4.18	4.43	4.29	4.50	4.55	4.30	0.38
A3	29.28	26.94	28.59	34.92	43.39	20.36	20.24	44.84	28.91	44.34	30.73	41.47	30.05	29.89	30.40	6.36
A4	58.76	50.79	58.20	54.84	67.84	40.24	40.36	57.27	51.15	69.50	71.37	70.83	67.13	58.36	62.37	9.66
A5	122.20	122.30	134.40	157.70	215.10	89.50	84.90	265.50	121.80	185.80	135.70	173.90	135.70	135.20	130.60	34.27

* All characters are significantly different at the 0.01 probability level.

\+ These character measurements were not replicated.

++ See table 7 for description of character codes.

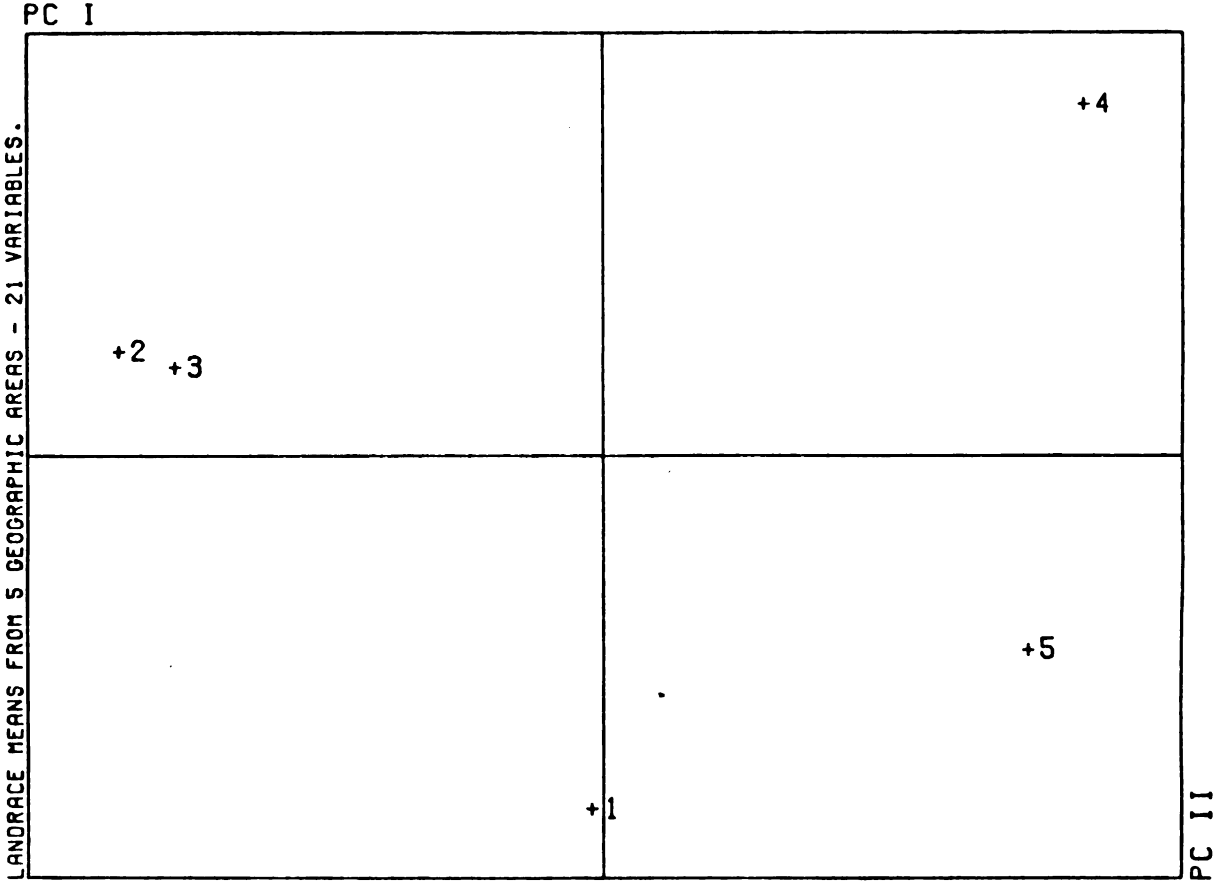

Figure 13: Plot of the first 2 standardized principal components based upon the area means of the 21 quantitative characters.

Table 14: Distances between areas based on the first 6 principal components derived from the 21 quantitative plant characters.

	Area				
	1	2	3	4	5
1	0	.8861	.9594	.9237	.9309
2		0	.8712	.9450	.8352
3			0	.9930	.9803
4				0	.8580
5					0

analysis they are not similar for a range of other characters.

The plot of the first two PC's based on site means of the 21 quantitative traits (Figure 14) accounted for 72.12% of the variance and revealed that there can be considerable homogeneity within a particular area (e.g. sites 1, 2, 3 all from area 1, appear very closely related) but also great heterogeniety (e.g. sites 7, 8, 9 all from area 3, are widely separated). This observation is supported by the the distances between sites within areas (Table 15) and by the intra-area mean distances presented in Figure 16. The sites appeared to separate into northern and southern clusters (Figure 14). For example, sites 10, 11, 12, 13, 14, and 15, the more southernly sites, constitute a fairly tight group in the upper right portion of the plot. The northern sites, while more dispersed, are mainly in the lower portion of the plot. The principal component analysis of the five phenological traits revealed a similar north - south clustering (Figure 15).

B) Environmental / Plant character associations.

Many statistically significant correlations between site variables and plant characters were observed (Table 16). Notably, several phenological characters were correlated with latitude, a finding which is also supported

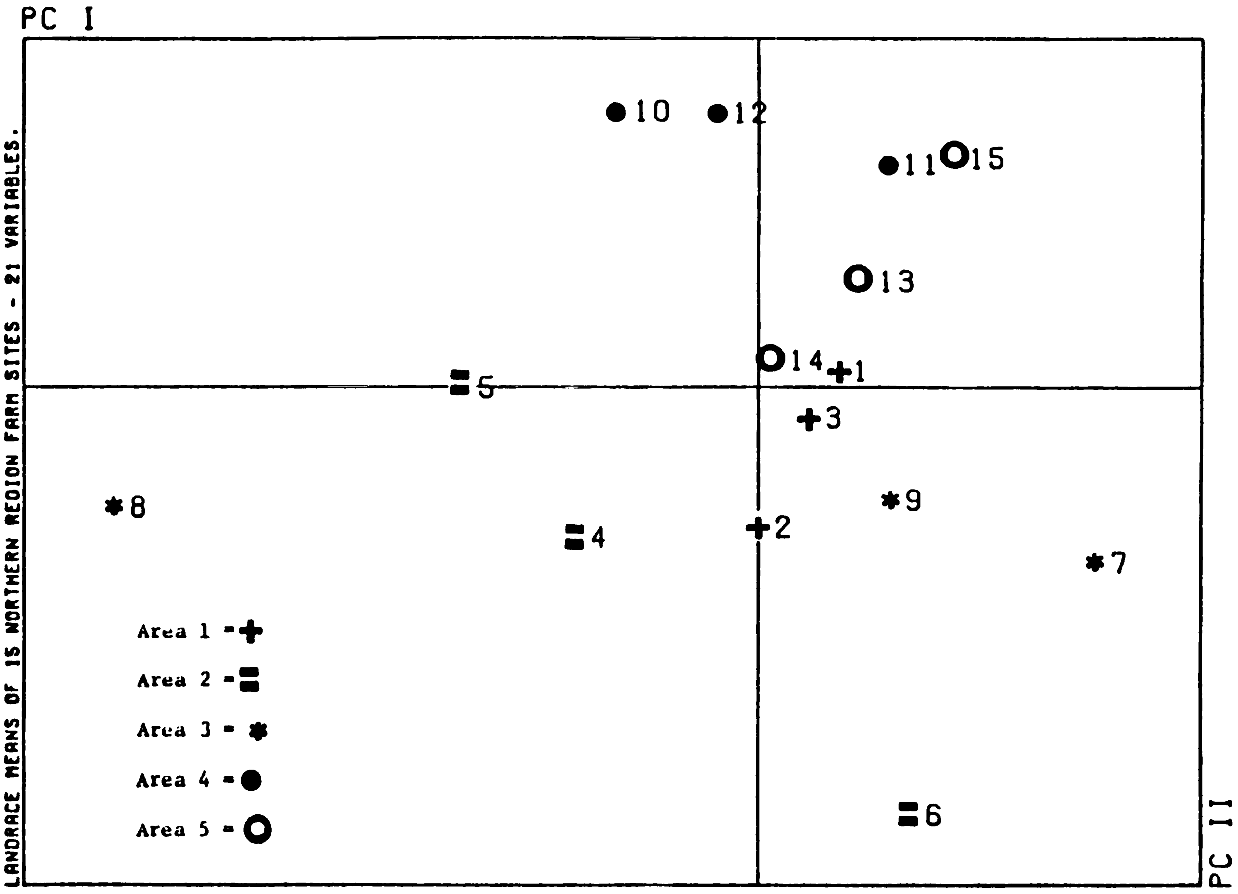

FIGURE 14: PLOT OF THE FIRST 2 STANDARDIZED PRINCIPAL COMPONENTS BASED UPON THE SITE MEANS OF THE 21 QUANTITATIVE CHARACTERS.

Table 15: Distances between sites within areas based on the 21 quantitative plant characters.

	Sites								
	1	2	3	4	5	6	7	8	9
1	0	.5918	.2646						
2		0	.5459						
3			0						
4				0	.6617	.5566			
5					0	.8690			
6						0			
7							0	1.2401	.8070
8								0	1.0646
9									0

	Sites					
	10	11	12	13	14	15
10	0	1.0429	.7914			
11		0	.6116			
12			0			
13				0	1.0628	.8372
14					0	.6964
15						0

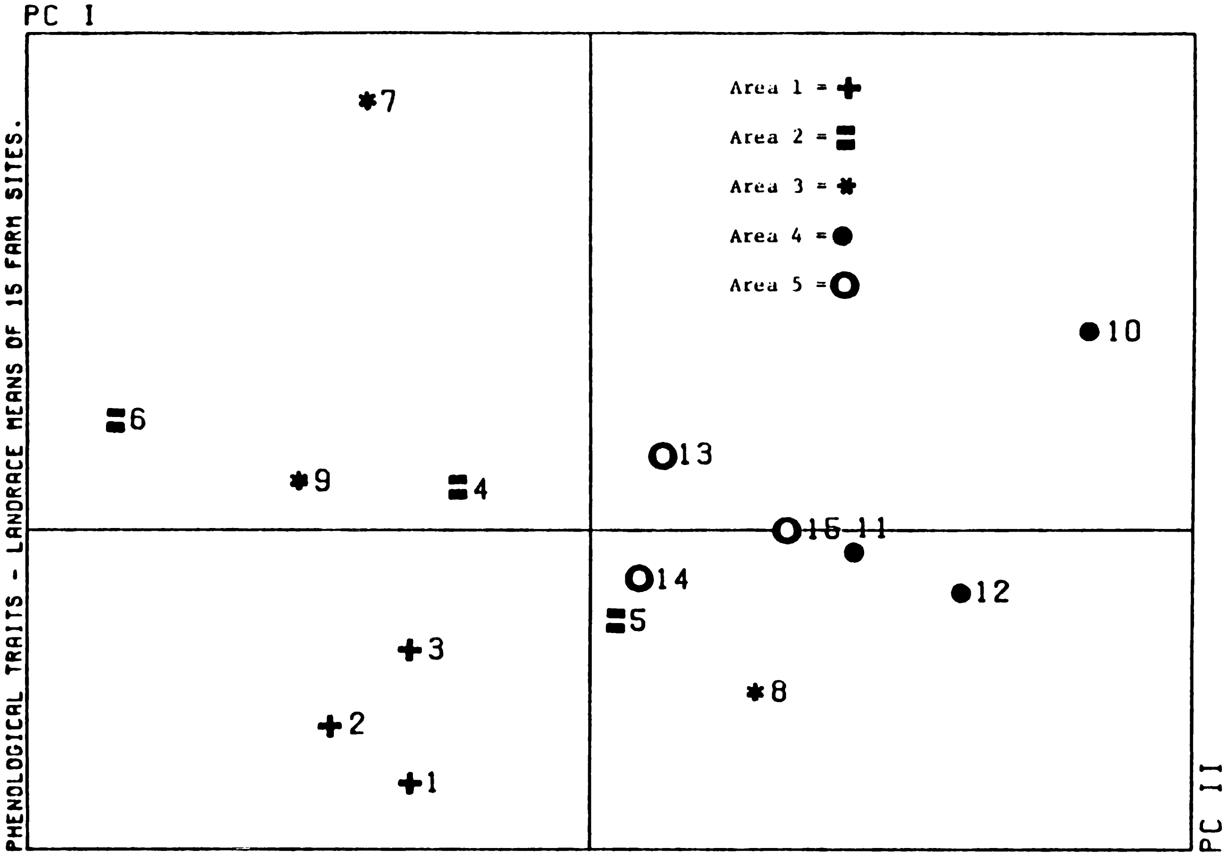

FIGURE 15: PLOT OF THE FIRST 2 STANDARDIZED PRINCIPAL COMPONENTS BASED UPON THE SITE MEANS OF THE 5 PHENOLOGICAL CHARACTERS.

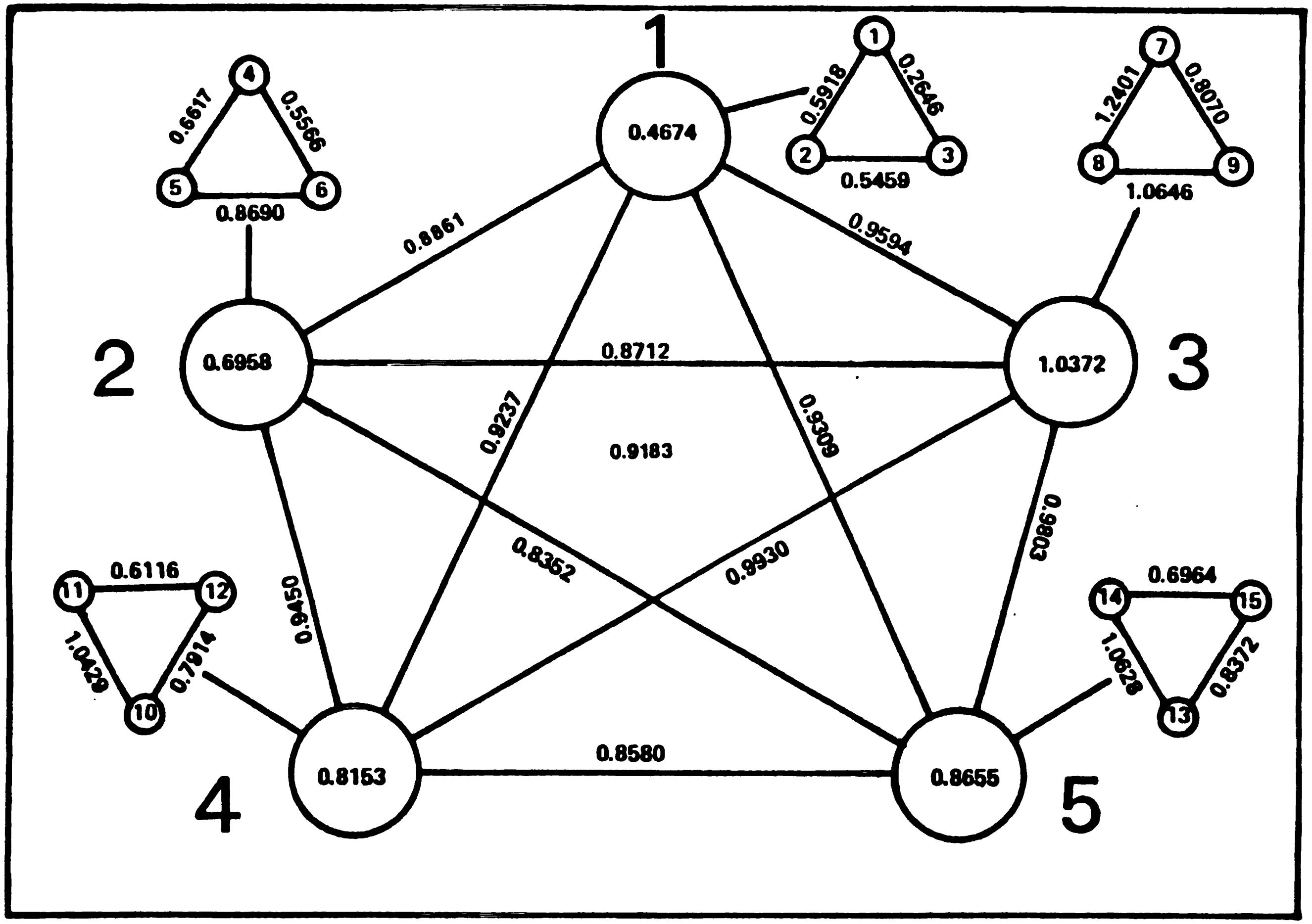

FIGURE 16: Distances between sites within areas (1-15) and between areas (1-5) based upon the standardized and normalized scores of the first 6 principal components derived from the site means of the 21 quantitative characters.

Table 16: Correlations between the 21 quantitative characters and selected site variables.

Character	Altitude	Sand %	pH	Phosphorous	Potassium	Nitrate	Heterozygosity level	Latitude
Days to emergence	-0.013	0.017	-0.151	-0.364	-0.328	0.173	0.536 *	-0.051
Days to first flower	-0.048	0.297	0.315	0.450	-0.118	0.411	0.517 *	0.714 **
Days to end of flowering	-0.123	0.550 *	0.360	0.564 *	-0.259	-0.173	0.555 *	0.544 *
Flowering duration	-0.141	0.502	0.194	0.351	-0.261	-0.713 **	0.271	0.031
Days to physiolog. maturity	-0.318	0.378	0.130	0.322	-0.253	0.205	0.616 **	0.587 *
Leaflet area	-0.098	0.296	0.201	-0.042	-0.519 *	0.481	-0.117	0.273
Leaflet length	-0.058	0.277	0.208	-0.112	-0.479	0.498	-0.115	0.259
Leaflet width	-0.091	0.279	0.117	0.007	-0.541 *	0.453	0.070	0.225
Leaflet shape	0.072	0.158	0.211	-0.203	-0.132	0.213	-0.253	0.150
Petiole length	-0.540 *	0.471	0.223	0.067	-0.446	0.243	-0.169	0.357
Hypocotyl length	-0.220	0.671 **	0.225	0.218	-0.710 **	-0.071	0.166	0.228
Seedling dry weight	-0.156	0.356	0.141	-0.030	-0.514 *	0.549 *	-0.207	0.353
Hypocotyl diameter	-0.081	0.305	0.109	-0.031	-0.602 *	0.589 *	-0.129	0.505
Nodes on main stem	-0.024	0.584 *	0.465	0.529 *	-0.316	-0.354	0.538 *	0.329
Seed length	-0.182	0.359	-0.079	-0.166	-0.683 **	0.274	0.008	0.182
Seed width	-0.211	0.438	-0.035	-0.091	-0.755 **	0.454	0.256	0.415
Single seed weight	-0.054	0.327	0.005	-0.159	-0.625 *	0.355	-0.182	0.284
Seeds per pod	0.008	-0.246	0.091	0.295	0.680 **	-0.250	-0.293	-0.075
Pods per plant	0.083	0.135	0.212	0.421	0.207	-0.263	0.574 *	0.138
Seed yield	0.058	0.565 *	0.334	0.545 *	-0.277	-0.073	0.471	0.528 *
Seeds per plant	0.526 *	-0.133	-0.053	-0.277	0.152	0.127	-0.014	-0.231

* , ** Significant at the 0.05 and 0.01 probability levels, respectively.

by the PC analysis which separated sites into northern and southern groups. Seven out of the eleven morphological traits were negatively correlated with potassium content of the soil, as was single seed weight. The number of seeds per pod was positively correlated with potassium content. Heterozygosity level exhibited several positive correlations with phenological characters. Seed yield was positively correlated with sand percentage, soil phosphorous, and latitude. Altitude, to some extent an indication of temperature in the tropics, showed a significant positive correlation with fecundity, and a significant negative correlation with petiole length.

C) Landrace population structure

The separate principal component analyses of the 15 landraces revealed an extraordinary complexity in the populational structure of most mixtures. Each landrace exhibited a wide range in relationships between its constitutive components. The distances for the two lines showing the greatest and the least degree of relationship from each site are presented in Table 17. In three cases the two lines most closely related were not similar for seed type, although similar seed types were present at these sites. In only one case were the two lines that were most distantly related actually the same seed type. Distances ranged from a low of 0.0749 to a high of 1.3215. Since

Table 17: Minimum and maximum distances between two-line pairs at each collection site, based on the 21 quantitative plant characters.

Site	Minimum	Lines	Maximum	Lines
1	0.1898	9,10	1.1184	2,17
2	0.1886	9,10	1.1542	20,23
3	0.1616	12,22	1.1973	16,25
4	0.2317+	1,4	1.1211	20,23
5	0.1612+	13,24	1.1821	6,25
6	0.1385	1,23	1.2102	10,22
7	0.1896+	15,24	1.2653	13,23
8	0.2261	4,12	1.2477++	20,21
9	0.1230	3,13	1.1969	10,22
10	0.0749	23,25	1.2707	5,8
11	0.0930	1,24	1.3215	6,13
12	0.1796	11,19	1.1898	10,17
13	0.1480	2,14	1.2662	10,25
14	0.2411	19,21	1.2137	2,6
15	0.1681	7,21	1.1557	4,25

+ Seed types of these pairs are different.

++ Seed types of this pair are the same.

beans are predominantly self-pollinating it would be expected that at least some lines would be identical by descent, i.e. pure lines. In the case of line pair 23 - 25, from site 10 and line pair 1 - 24, from site 11, for example, this is very likely the case. However, there were other seed types which, though appearing homogeneous did not appear closely related according to the PCA distance. Five of these homogeneous seed classes were analysed further. Table 18 and 19 present the separate analyses of variance for the 18 replicated characters measured on homogeneous seed classes from two sites. The brown and purple seed types, from site 1, were found to be significantly different for three traits and one trait, respectively. The brown types differences were all in agronomic traits which are inter-related by mathematical transformations and are thus highly associated with each other. Thus, the brown and purple seed classes from this site do display a high level of homogeneity for quantitative, as well as qualitative traits. Homogeneous seed classes, however, did not always appear similar for metric traits. The yellow seeded class from both site 1 and site 6 and the tan/red class from site 6 displayed many significant differences in all three character categories, thereby suggesting that these homogeneous types are, in fact, not pure lines.

The average distances between individual lines in each of the five phenotypically similar seed types are given in

Table 18: Analysis of variance for the 18 replicated plant characters in three homogeneous seed types from collection site 1.

Character code ++		Seed type		
		Brown	Purple	Yellow
	Df	11	6	4
			Mean squares	
P1		0.51	0.27	1.07
P2		2.76	3.10 *	2.27 *
P3		2.82	6.76	8.23
P4		5.06	16.33	5.57
P5		14.13	11.83	8.23
M1		90.50	88.64	268.88 *
M2		1.10	2.45	4.78 *
M3		1.03	0.83	1.18
M4		0.02	0.09	0.04 *
M5		1.28	0.23	0.04
M6		0.37	0.93	1.39
M7		0.10	0.06	0.31 *
M8		0.59	0.55	1.00 *
A1		0.005 **	0.001	0.0001
A2		0.10	0.16	0.25
A3		75.80	20.05	78.36 *
A4		424.36 *	150.40	432.00
A5		1272.80 *	316.49	2539.69 **

*, ** Significantly different at the 0.05 and 0.01 probability levels, respectively.

++ See table 7 for description of character codes.

Table 19: Analysis of variance for the 18 replicated plant characters in two homogeneous seed types from collection site 6.

Character code ++		Seed type	
		Tan / red	Yellow
	Df	10	13
		Mean squares	
P1		2.80	1.50 *
P2		3.21	2.86 *
P3		2.32	18.54 **
P4		4.63	29.92 **
P5		12.34 *	8.29
M1		186.18 *	41.50
M2		1.67	0.76
M3		1.32	0.82
M4		0.04	0.06 **
M5		0.79	0.98 *
M6		0.74	0.95 *
M7		0.21 *	0.28 **
M8		0.30	0.56
A1		0.004 **	0.008 **
A2		0.33 *	0.29 **
A3		64.21 **	55.94 **
A4		194.94 *	114.36
A5		997.88 *	742.93 *

*, ** Significantly different at the 0.05 and 0.01 probability levels, respectively.

++ See table 7 for description of character codes.

Table 20. The brown and purple classes, which displayed few differences for the individual traits, also appear most closely related and have the smallest standard deviation. The remaining three groups have higher mean intra-class distances and higher standard deviations.

Since the usual range of distances for different degrees of relationship is unknown based on these 21 traits, the distances between the four Michigan lines included in this study whose pedigrees are known are presented in Table 21. Black Magic, Domino, and Swan Valley were all derived from one original cross and are thus full sibs. They have, however, undergone several cycles of selection for slightly different characteristics. Nevertheless, the small distance between Black Magic and Domino (0.2595) testifies to their close relationship and similar black seed type. The distances between these two and Swan Valley, a navy bean, is expectedly a little greater. These three lines are distantly related to Seafarer according to this analysis, an observation supported by their known lack of pedigree relationship.

The brown-seeded types from site 1, based on the AOV's and their average intra-group distance, are closely related, suggesting that they may be sister progenies of a single pure line. Table 22 presents the PC scores for several two-line pairs from this group. It can be seen that even though

Table 20: Mean distance and standard deviation between lines within each of five homogeneous seed types.

Site / Seed type		Number of lines	Mean distance	Standard deviation	Number of significantly different traits in the AOV's.
1	Brown	12	0.5573	0.1540	3 (A1, A4, A5)
1	Purple	7	0.6246	0.1441	1 (P2)
1	Yellow	5	0.7459	0.1600	8 (P2, M1, M2, M4, M7, M8, A2, A5)
6	Tan / red	11	0.6629	0.1801	8 (P5, M1, M7, A1, A2, A3, A4, A5)
6	Yellow	14	0.6486	0.2307	12 (P1, P2, P3, P4, M2, M5, M6, M7, A1, A2, A3, A5)

Table 21: Distances between Michigan lines, based on the 21 quantitative plant characters.

	Domino	Black Magic	Swan Valley	Seafarer
Domino	0	0.2595	0.7335	1.1827
Black Magic		0	0.5802	1.0601
Swan Valley			0	1.100
Seafarer				0

Table 22: Normalized scores for the first 6 principal components, and distances between three pairs of brown-seeded lines from site 1.

Line	Distance	Principal component					
		1	2	3	4	5	6
7	0.2215	-0.3130	0.1528	-0.1961	-0.0305	0.0779	-0.0417
22		-0.2870	0.1213	-0.0159	-0.0826	-0.0015	-0.1186
Difference		0.0260	0.0315	0.1802	0.0521	0.0794	0.0769
3	0.4697	-0.1340	0.1545	0.3293	0.2387	0.2325	0.1457
18		-0.1918	0.1273	0.0982	0.0291	-0.0224	-0.0874
Difference		0.0578	0.0272	0.2311	0.2096	0.2576	0.2331
12	0.5785	-0.0066	-0.1673	0.1508	-0.1360	-0.1251	0.3792
13		-0.0631	-0.1078	0.1072	-0.2161	-0.2804	-0.1644
Difference		0.0565	0.0595	0.0436	0.0801	0.1553	0.5436

two lines may appear closely related based on the AOV's and the PCA, they may still display differences on individual PC axes.

The scatter plots of the first two PC's for each site are presented in Appendix B. These plots accounted for an average of 52.0% of the variance. In general, distinct clusters were observed which consisted of phenotypically similar seed types. The landraces, taken as a group, appear to represent a continuum, beginning with simple mechanical mixtures, proceeding to landraces exhibiting incipient genetic intergradation of major seed classes, then to landraces showing distinct "hybrid swarms" and finally to landraces appearing to consist of predominantly recombinant types. Examples of each of these stages are depicted in Figures 17 - 24. Segregating lines are denoted by a dash.

Figure 17 and 18 (sites 8 and 11), depict simple mechanical mixtures. None of the lines from these landraces segregated and distinct clusters of fairly uniform seed types were observed. Sites 2 and 7 are also examples of simple mixtures (Appendix B).

Figures 19 through 22 portray the first step towards introgression. In each of these landraces at least one line segregated, and in each case the positioning and the phenotypes of the recombinant seed types suggests the putative parents of the segregating line. Thus for example, in Figure 20, site 1, line 12 appears to have been the

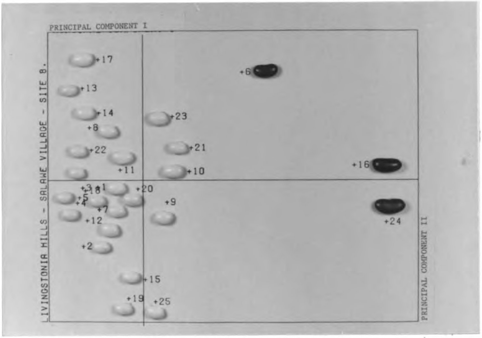

Figure 17: Principal component plot of the landrace from site 8 - an example of a simple mechanical mixture.

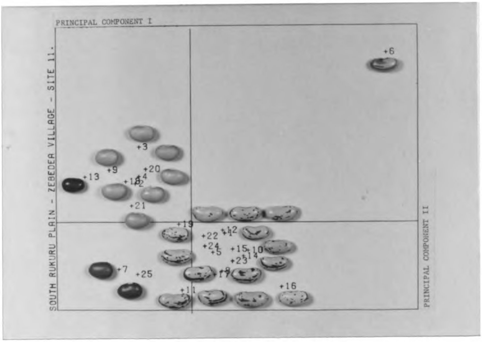

Figure 18: Principal component plot of the landrace from site 11 - an example of a simple mechanical mixture.

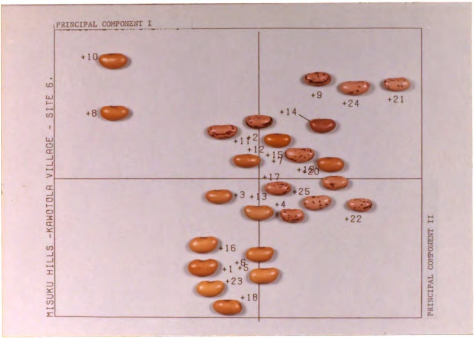

Figure 19: Principal component plot of the landrace from site 6 - an example of incipient genetic intergradation.

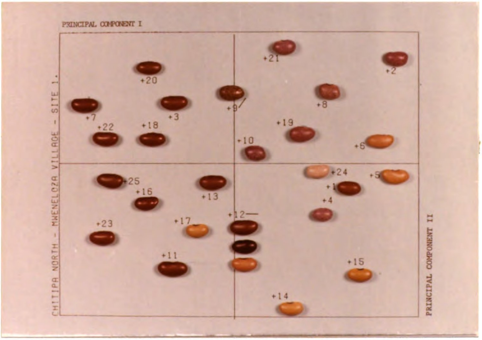

Figure 20: Principal component plot of the landrace from site 1 - an example of incipient genetic intergradation.

result of a natural outcross between a yellow and the brown-seeded type. Line 9, at the same site, appears to be the result of a cross between a brown-seeded and a purple-speckled type. Figure 21 (site 5) depicts this incipient genetic intergradation even more clearly. In this landrace there are recombinants which appear to have resulted from three crosses between three major seed classes at this site. Line 14 was probably a cross between a zebra-striped bean and the tan/red mottle bean (line 6). Line 9 seems to be a cross between one of the small, hilum-spotted types and a zebra-striped bean. Line 16 was likely a cross between a solid brown bean and a zebra type. Line 20 may be another segregant from the tan/red mottle bean and a zebra type. For Figure 22 (site 14) the segregating progeny from lines 15 and 16 were unavailable, however this landrace too exhibits a pattern of nascent genetic intergradation. Other examples of this early stage are sites 3, 9, 13 and 15 (Appendix B).

Figure 23 (site 4), appears to be an example of a later stage of genetic intergradation. A distinct cluster, actually a "hybrid swarm", is apparent in this landrace, consisting of lines 5, 8, 9, 18, 19, and 24. Progeny of four of these segregating lines were available and they clearly show that a unique seed class has arisen. This farm also appeared to have two distinct yellow seeded types.

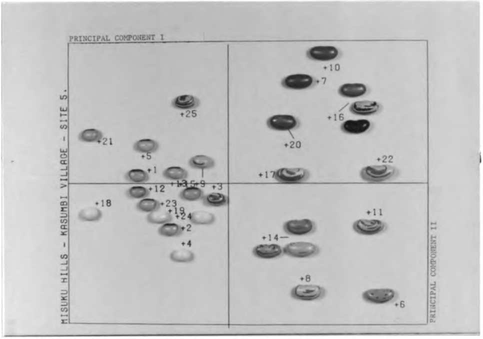

Figure 21: Principal component plot of the landrace from <u>site</u> <u>5</u> - an example of incipient genetic intergradation.

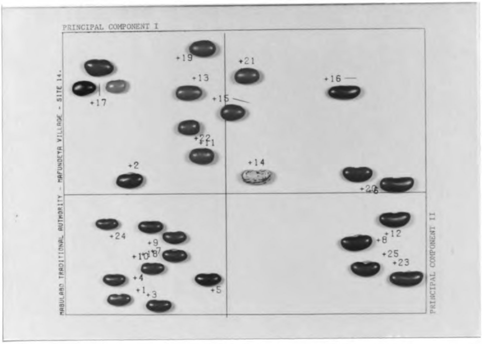

Figure 22: Principal component plot of the landrace from <u>site</u> <u>14</u> - an example of incipient genetic intergradation.

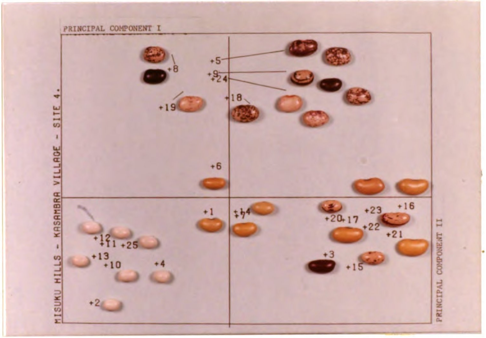

Figure 23: Principal component plot of the landrace from <u>site 4</u> - an example of a later stage of genetic intergradation where a 'hybrid swarm' has formed.

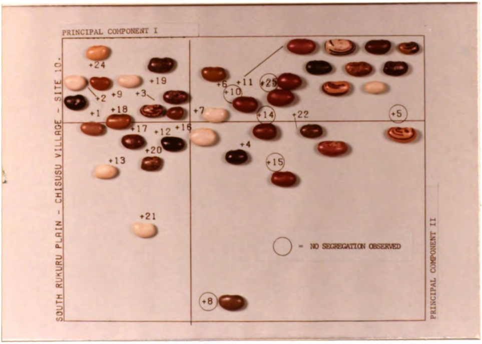

Figure 24: Principal component plot of the landrace from <u>site 10</u> - an example of very extensive genetic intergradation.

Figure 24 (site 10), depicts a truly complex array of new seed types which have arisen as a result of outcrossing. Eighteen of the twenty-five lines in this landrace segregated. Viewed broadly, this landrace appears to have consisted, at one time, of reddish and purple lines (to the right in the plot) and brown and white types (to the left). Considerable genetic intergradation has already occurred as shown by the many "off-types". Site 12, where 17 of the 25 lines segregated also represents this later stage of genetic intergradation (Appendix B).

Chapter 5

DIVERSITY IN MALAWIAN BEAN LANDRACES

Discussion

A) Variability in the landraces.

This study arose from a simple observation - bean landraces in Malawi were found to be extremely diverse for seed color, pattern, size and shape. As far back as 1938 Harlan and Martini observed that mixtures of self-pollinating varieties quickly became dominated by one or two genotypes. More recently, Vieira (1975) found that bean mixtures consisting of six homozygous lines were dominated by a single line after just four generations. Yet bean mixtures are present in Malawi and apparently have existed for a very long time. How can these conflicting observations be reconciled? What forces are generating the variability in these bean landraces, and what factors are influencing its maintenance? This study has addressed four specific questions. First, what is the extent of the genetic diversity in the Malawian bean landraces and is there a pattern to the variation over the northern region? Secondly, what, if any, are the advantages of variability for the specific characters measured in these landraces? Thirdly, is there evidence for site-specific or regional adaptation to certain environmental variables? And lastly, what role does outcrossing play in generating and maintaining the variability in the landraces?

This study has confirmed that a vast store of genetic variability is extant in the Malawian bean landraces for both qualitative and quantitative characters. Seed characteristics - visually the most striking indication of this variability - were found to be extremely diverse within individual landraces. However, a broad regional pattern of variation is evident. The landraces from the northernmost sites consisted of predominantly yellow, brown, or tan/red mottled beans. The more southernly sites grew primarily reddish beans. Whether this demarcation in types is due primarily to environmental forces or to consumer preferences cannot be answered here. Kaplan (1981) has observed that "seed variations serve as genetic markers that enable humans to supply the energy for selection that maintains the observed diversity". The existence of a vernacular for specific seed variation in Malawi indicates that preferences have developed for certain seed types. The presence of cosmopolitan seed types (tan/red mottle) suggests that a distribution network does or has existed and that types having general consumer acceptance (or environmental adaptation) may spread over a wide area. Thus, either consumer prejudice or environmental factors likely do play a role in the present-day distribution of seed types. The possibility that the introduction of seed types into new areas has been completely random should, in general, be discounted. The Livingstonia Hills area, however, where several anomolous mixtures occurred,may be an area where there has been a more random introduction of seed types. These unusual mixtures, perhaps not coincidentally, were collected within 20 miles of the Livingstonia Mission. This mission was founded in 1881 and has had a considerable impact on the education of the local people. A distinct possibility exists that this mission has been responsible for the introduction of beans from other areas of the country and even from British colonies in other parts of Africa. The preponderance of white pea-beans at site 8, similar to those produced on a large scale in Tanzania in the late 1930's, would tend to support this hypothesis.

Segregation of bean lines was observed in all but four landraces. In two landraces, those from sites 10 and 12, 70% of the lines were found to be segregating for seed type, flower color or hypocotyl color; other quantitative traits were also likely segregating. The great range of seed types which may arise from a single heterozygous seed was documented in Part I of this thesis. Thus, it may not be necessary to assume an inordinately high rate of outcrossing in order to account for this great seed diversity. Although the outcrossing estimate of 1-2% arrived at in the outcrossing estimation plots may be low due to the low proportion of climbing-longer flowering types in the study, even this rate would have a dramatic effect in a population of 5,000 to 10,000 plants. Finally, since the genetic expression of seedcoat lags behind one generation, a farmers attempt at removing "off-types" from his population would be, in good part, thwarted. And even if a farmer were to attain a uniform seed type an occasional outcross from his neighbors' field - often only a few meters away - would again contaminate his stock. Indeed, from this point of view, the maintenance of mixtures appears less puzzling than the maintenance of pure lines.

The lack of any distinct pattern for flower colors and hypocotyl color probably indicates that there is little, if any, human or environmental selection for these traits. Segregation of both white and colored flowers from several lines would suggest that if there is a preference for flower color by pollinating bees, it is not exclusive. Relatively high proportions of the three hypocotyl colors in every area may suggest the existence of a balanced polymorphism for this trait in many landraces.

Indeterminate beans predominate in the northern region. This is not surprising since the vast majority of farmers grow their beans in association with maize, and climbing bean are probably better adapted to this system. However, it is interesting that all but three landraces also contained determinate beans. Vieira (1975) in a study of a six component mixture, found that climbing beans quickly dominated the mixture; the bush beans were reduced to 0.5% by the fourth generation. He believed that the determinate types would have been eliminated in one more generation. Vieira, however, grew his mixtures at a population of 250,000 plants per hectare. Under this high density, competition between bean plants would be extreme. Vieira mentions that Brazilian farmers usually maintain beans at between 15,000 and 75,000 plants per hectare associated with 20,000 to 45,000 maize plants. In Malawi, beans are grown at between 20,000 and 60,000 plants per hectare in association with maize (Edje et. al., 1980). It is clear that the the competition in a Malwian bean/maize field, where there is an average of 3-4 bean plants per square meter, is not intraspecific. That is, beans do not compete with beans so much as they compete with maize. As the ecological niches of these two species are decidedly different, it is understandable how both bush and climbing types may coexist in a landrace. Indeed, they have different "strategies" for competing with maize. The bush beans are generally earlier and thus mature before the maize has shaded the lower zones in a field. Indeterminate beans, in contrast, climb up the maize, thereby avoiding shading stress to some degree. Ultimately, since direct competition between bean types is avoided, both may survive. Several sites, (e.g. sites 4, 9, 14) contain high proportions of both bush beans and climbing beans. This suggests that the maize landraces at these sites are perhaps less vigorous, that they are planted later than beans, or that the farmer plants maize at relatively low density.

Phenological characters, in general, show a high level of variability within landraces, between sites and even between areas. Days to first flowering, days to end of flowering, and days to physiological maturity were significantly different between areas at the 0.01 probability level. Kaplan (1981) found that bean mixtures from Oaxaca, Mexico contain components with markedly different germination rates. He observed that a mixture may extend the germination period 2.3 times over that of a single variety. The components of Malawian landraces studied here differed in the rate of emergence from 10 to 21 days. In Malawi, where the first rains are often interrupted, this emergence differential could have obvious advantages. The variability in other phenological traits, by spreading out the occurrence of the critical flowering and seed-filling periods, would similarily reduce the risk of crop loss. This, in fact, has a direct corollary to Imam and Allard's (1965) wild oat populations wherein they believed the variability increased the adaptive peaks which the population could occupy and allowed a more efficient use of the available moisture, light and nutrients.

Great morphological diversity is evident in these landraces for all 11 traits measured. Considerable adaptive importance may be associated with leaf size when a genotype is competing with maize for available light. Similarly, petiole length differences may play a role in the positioning of the leaf to the incidence of sunlight, an important capability under shaded conditions. Greater hypocotyl diameter might be expected to be an advantage where beans are grown up on ridges, as they are in Malawi, where a tendency toward lodging may exist. Despite these supposed advantages for a certain morphology, the landraces are rarely uniform for a particular trait. This diversity, again, is likely a result of the presence of many adaptive peaks in these populations. Thus, although small leaves may more easily orient to the sunlight, they are associated with small seeds and thin hypocotyls which may have disadvantages with respect to beanfly (Ophiomyia phaseoli) attack. Conversely, large leaves and long petioles may hinder leaf orientation, but they are associated with large seededness which generally results in early vigorous seedling growth. Thus, over the course of the year from sowing, seed-filling, and harvesting to storage and consumption, each morphological configuration may possess certain advantages which permit it a selective edge.

Yield and yield components, of great importance to modern plant breeders, may be of less interest to Malawian farmers. Occasionally farmers will mention that a certain type is "high yielding" but much more often qualitative reasons for growing a certain seed type will be offered (e.g. "good taste", "store well", "like the color"). It is striking, and puzzling, that great differences in fecundity exist between lines in individual landraces. Small seeded types generally produce more seeds per plant than large seeded types. And yet, in most mixtures, large seeded types predominate. Part of the explanation may be that farmers say they prefer large seeds and hence they may be applying a strong selective pressure for these. Why do they maintain small seeded types at all then? This again may fall into the elusive arena of consumer preferences. Farmers will occasionally cite qualitative reasons for growing certain small seeded types (e.g. small, hilum-spotted types are said to be drought resistant). Overall though, Malawian farmers simply may not care if their landrace is uniform for seed size; they appear to apply very little selection for other traits either. One dichotomy may be presented here. It is interesting that in maize, a difficult crop in which to maintain purity, Malawian farmers desire (and succeed in maintaining) a very uniform grain type. A whitish, floury seed which has the "right" qualities for making nsima is preferred. Now, maize and beans form the primary carbohydrate and protein source in Malawi and are thus culturally important. Why the farmers insist on great uniformity in one and seem to prefer great diversity in the other is a puzzle. Especially since selection for uniformity in a self-fertilizing species, such as the common bean, should be relatively easy.

Storage is likely a critical stage in the maintenance of bean mixtures. Roos (1984) observed differences in viability in an eight-variety mixture after storage under high temperature and high humidity - conditions similar to those on a Malawian farm. Using computer simulation, he found that after five generations the mixture was dominated by Cherokee Wax, a black-seeded bean. However, even after fifteen generations, two other varieties still persisted. The two white-seeded lines in his study were rapidly eliminated in the first few generations. His study may provide a clue to the persistence of certain types in the Malawian mixtures even though they are less fecund than other lines. High temperature, high humidity, and perhaps most importantly bean weevil attack, may be very potent differential selective mechanisms which are operating to maintain the polymorphisms in these bean populations.

To sum up this discussion of individual landrace diversity, it may be said that the presence of the extraordinary variability in Malawian landraces documented in this study indicates that specific advantages must exist for bean mixtures. These advantages may be due to a buffering effect which enhances disease and insect tolerance, or to a differential response to drought or light stress. The ability of a landrace to spread its nutrient, moisture, and light requirements over time by having differing phenological "schedules" may also confer specific advantages. Finally, the advantages perceived by the farmer are very centrally involved here. Consumer preferences are often fickle, but they too may be based on very perceptive observations of the crop ecosystem. Still, it is not beyond reason that farmers have simply grown to like the colors and patterns of their diverse landraces and thus maintain them, in part, for aesthetic purposes. The introduction of pure lines or homogeneous seed types that may replace these complex mixtures should be viewed with great circumspection.

Although considerable variability may exist within individual landraces, there are regional patterns of diversity which were uncovered by the principal component analyses. Surprisingly, areas which shared similar seed types were not always similar when viewed multivariately. For example, area 2 (sites 4, 5, 6) and area 5 (sites 13, 14, 15) were most closely related according to the principal component distance analysis. Area 2, however, consists of primarily yellow, mottled, and small seeded white beans and tan beans. Area 5 contains mostly large seeded reddish beans. Apparently these areas share many similarities for other agronomical or phenological traits. This observation reinforces the fact that seed characteristics alone are but a small indication of the genetic architecture of these landraces.

The principal component analysis of site means uncovered a fairly sharp differentiation between the nine, more northernly sites and the six southernmost sites. The southern sites formed a fairly tight cluster, while the northern sites, though more heterogeneous, formed another cluster. Days to first flowering, days to end of flowering and days to physiological maturity were significantly different between areas and the PCA of the five phenological traits alone exhibited a similar and even clearer differentiation between the northern and southern landraces. The possibility that there has been specific adaptation to daylength in these landraces will be discussed in the section on environmental / plant character associations.

The PCA of site means also revealed a pattern of diversity within areas. The landraces within areas may be very similar (e.g. sites 1, 2, 3; sites 10, 11, 12; and sites 13, 14, 15), but they may also be extremely dissimilar as in sites 4, 5, 6 and sites 7, 8, 9. The possibility that landraces 7, 8, and 9, which were collected near the Livingstonia Mission, may have been influenced by recent European introductions has already been mentioned. Why sites 4, 5, and 6 are so different from each other when they were collected within a relatively small area is unclear. Genetic drift may provide one explanation. Another possibility is that the extreme ethnic diversity in the Misuku Hills (over six language groups occupy this area) has given rise to varied cultural preferences for seed types.

To sum up, there appears to be evidence for broad regional adaptation in these landraces. However, individual farmer preferences, recent outside influences of Europeans, and ethnic differences within certain areas have also likely played a role in combining the contemporary components of the mixtures.

B) Environmental / Plant character associations

The many significant correlations between environmental variables and plant characters indicate that there is some site-specific adaptation occurring in the Malawian bean landraces. Several phenological traits (days to first flowering, days to end of flowering and days to physiological maturity) were significantly positively correlated with latitude, a finding supported by the PCA. The more southernly landraces were generally later for these traits. Daylength difference between the northernmost and the southernmost areas is only 10 minutes on January 15, which would be the approximate date of flowering for beans planted in early December. That the landraces are adapted to such small photoperiodic differences is not wholely unlikely. Bunting (1975) in a paper on the phenology of crops, has stated that very specific adaptation to photoperiod exists in sorghums in northern Nigeria. The sorghums there flower progressively later as one proceeds northwards over a fairly short distance - 250 to 300 miles.

There may be other reasons beyond photoperiodic adaptation which are involved with these phenological traits, however. It is possible that the farmers prefer earlier beans in the north because they take better advantage of the rainfall regime or they fit in better with their farming system. This correlation with latitude may then be the result of agricultural practices of the various ethnic groups rather than a direct environmental response.

Another significant, positive correlation is that between soil phosphorous level and seed yield. Haag, Adams, and Wiersma (1978) found differential response for phosphorous use efficiency in 124 dry bean genotypes from North and Central America. They suggested that "The response of a genotype and the nutrient supplying capacity of its native soil may not be unrelated". This appears to be the case in these 15 landraces. The landraces from high phosphorous soils are higher yielding, at least when grown under high phosphorous conditions as they were in this experiment. If a high phosphorous level does indeed exert a positive selective force for yield, it would be necessary to assume that the landraces were grown on high phosphorous soils continually for directed selection to occur. Since most farms in northern Malawi are quite small, it is likely that considerable soil homogeneity does exist from year to year as a farmer rotates her fields and that a consistent selection pressure is present.

Many morphological characters were significantly negatively correlated with potassium content of the soil. High potassium was associated with small leaves, small seeds, narrow hypocotyl, short hypocotyl, short petioles and few nodes on the main stem. No obvious connection is known to explain these correlations, but the high number of correlations suggests that potassium level may be exerting a strong selective force on the morphology of individual landraces.

The percentage of lines segregating at each farm ("heterozygosity level") is positively correlated with days to emergence, days to first flower, days to end of flowering, days to physiological maturity, nodes on the main stem, and pods per plant. Seed yield is also positively, though not significantly, correlated with heterozygosity level. Interestingly, seeds per plant is not correlated with heterozygosity ($r = -0.014$). These correlations indicate that the landraces with a greater occurrence of recombination generally contain later maturing bean lines. It was observed during the course of this study that segregating lines often produced progeny which were taller and much more vegetative than the norm. The lack of correlation between fecundity and heterozygosity level suggests that heterozygote advantage for fitness is not present in the landraces studied here.

C)Landrace populational structure

The separate principal component analyses of the 15 landraces, in many cases, revealed a considerable complexity in the interrelationships between the individual bean lines. Although seed characteristics were not used in these analyses, similar seed types, in general, clustered together indicating a degree of homogeneity within seed classes. Since beans are a predominantly self-fertilizing species it is to be expected that a landrace will contain some lines which are identical by descent, i.e pure lines. In many instances this is undoubtedly the case. However, very large PC distances were observed between many line pairs which shared a similar seed type. This suggests that these lines, though phenotypically the same for seed type, actually carry different genes for the array of other characters recorded in this study. Before discussing quantitative differences within such homogeneous seed classes, one example of a striking qualitative difference will be noted. The landrace from site 3 contains two lines which are identical for seed type - medium-large, oval and solid white. Line 2 however, is a determinate bean and line 25 is indeterminate and a strong climber. Such gross qualitative differences within a seed type were observed for flower color as well.

It would be valuable to know what PC distance is expected between two entries of the same pure line in a study such as this. In other words, what sort of error exists. However, since several pure lines pairs were not included in this study, such a "benchmark" distance is unavailable. Lacking this, it may be highly subjective to set a specific distance below which lines may be considered pure lines and above which they may be assumed to be different. Adams (1977), in his principal component analysis of U.S. bean cultivars, found an average distance of 0.2048 between Red Mexican lines known to be closely related (Wright's relationship coefficient, R = 0.8750). This analysis, however, was based on very different morpho-agronomic and chemical traits than were used in this study and it may be inappropriate to use this distance in evaluating relationships among components in the Malawian landraces. The distances between the four Michigan lines included in this study are probably the closest standard available that can serve this purpose. Domino and Black Magic, phenotypically very similar, were derived from the same original cross, as was Swan Valley. Although these lines have undergone selection for slightly different traits, they can be expected to share many genes in common. The relatively small distance of 0.2595 between Domino and Black Magic indicates a close relationship. The distances between Black Magic and Swan Valley (0.5802) and Domino and Swan Valley (0.7335), however, indicate that selection within a full-sib family can result in considerable differences between lines and hence relatively large distances.

The minimum distance between line pairs from each landrace ranged from 0.0749 to 0.2411. In three cases these pairs did not share a similar seed type. Nevertheless, a distance of 0.0749 (site 10, lines 23-25) or 0.0930 (site 11, lines 1-24) very likely indicates that the members of these pairs are actually derived from the same pure line.

Many homogeneous seed classes were found to contain lines, between which the average distance was considerably higher than these pairs. Five such classes were analysed further. Site 1 contains 12 lines which shared an identical brown, oval seed type, 7 lines which shared a purple-speckled seed type, and five which shared a solid yellow seed coat. Site 6 contains 11 lines of tan/red mottled type and 14 lines of a similar yellow oblong type as that from site 1. Separate AOV's for the 18 replicated, quantitative characters for each of these seed classes revealed both homogeneity and heterogeneity within different classes. For example, the brown class and purple-speckled class from site 1 showed very few significant differences between lines for the 18 traits, indicating that they may, in fact, be pure lines. The remaining three seed classes, however, had significant differences for very many traits suggesting they are far from being pure lines. The average distance between the brown types was 0.5573, that between the purple types 0.6246. The more heterogeneous classes had larger distances: 0.6486 (yellow's, site 6), 0.6629 (tan/red mottle) and 0.7459 (yellow's, site 1). The standard deviations within the classes with larger distances were considerably higher than in the homogeneous classes. These analyses demonstrate two things. First, very homogeneous seed classes may have average intra-group distances much higher than the low distances which were mentioned earlier as being indicative of a pure line. Secondly, phenotypically similar seed classes may contain lines which are extremely variable for an array of quantitative traits. Thus, similar seed type among a group of lines in a landrace should not be taken as evidence that they are pure lines. Bean researchers in Malawi should not rely solely on seed diversity when evaluating the potential variability in a landrace.

Indeed, even within the very homogeneous brown seed class from site 1, where few significant differences were observed, considerable variability may exist. The normalized scores for the first six PC's revealed that although two lines may be closely related, as judged by the PC distance (e.g lines 7 and 22, with a distance of 0.2215), their scores may vary widely on individual axes. Since a PC axis, in this study, is a multivariate portrayal of a particular germplasm aspect, these data suggest that these brown lines, though assumed to be pure lines, may actually differ in many ways not uncovered by a univariate analysis.

At the beginning of this discussion two conflicting observations were presented. One is that experimental mixtures of varieties of self-pollinating species are generally found to be quickly dominated by the most competitive line. The other observation - that which has been documented in this thesis - is that mixtures of diverse bean lines are present in Malawi and have apparently persisted there for a very long time. The principal component analyses of the individual landraces, I believe, reveal a possible explanation for this paradox.

The principal component analyses of the 15 landraces uncovered what appear to be several stages of genetic intergradation*. This process probably prevents one line from dominating the landrace. The degree of genetic intergradation likely depends on three factors: the number of seed types originally composited by the farmer, the rate of outcrossing which is present in the area, and the survival rate of the recombinants. Sites 8 and 11 are examples where distinct groups of more or less pure types are being maintained. These types may have recently been

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* The term 'genetic intergradation' refers to the gradual process of gene exchange resulting from natural hybridization between genotypically different entities in a landrace.

composited by the farmer or there simply may be little or no outcrossing occurring in these areas. Sites 1, 5, 6, and 14 exhibit incipient genetic intergradation of the major types being grown at these farms. As the new recombinant lines begin to segregate, and if the segregants are well adapted, we would expect "hybrid swarms" to develop and to occupy presently unoccupied ecological niches in the population. If a principal component plot may be viewed as a multivariate portrayal of the present environmental niche of the bean mixture, then the gaps between seed type clusters would represent as yet unoccupied adaptive peaks within the niche. Site 4, then, is an example where a hybrid swarm has developed in an otherwise unoccupied adaptive peak. This swarm, at present consisting of a small number of segregating progeny, may be expected to expand and along with recombinants from other natural crosses, eventually "fill in" the gaps in the environmental niche of the bean mixture at this particular site. The principal component plot of site 10 is perhaps a portrayal of such exploitation. Here the many recombinants, along with the nonsegregating and apparently "original" lines, are well distributed throughout the plot and analogously throughout the environmental niche at this site.

Thus, in a sense, a continuum of genetic intergradation is present in these bean landraces. However, it should be said that it is probably not likely that all landraces are progressing towards the extensive genetic intergradation found at site 10. Rather, this site, along with site 12, may be the result of an inordinately high outcrossing rate or a relatively diverse original population. Landraces such as those from sites 8 and 11 may remain as simple mixtures as the result of a lack of outcrossing or possibly due to a very vigilant farmer who is selecting out off-types.

In conclusion, it appears that outcrossing is a powerful mechanism by which variability is generated and maintained in these populations. Although not all landraces seem to be influenced by outcrossing, those that are not are generally much less diverse for seed types and a range of other characters. Outcrossing is probably a recurrent force in many bean populations and is likely resulting in variability beyond even the original intention of the farmer when she first mixed several bean types. The result of this outcrossing is not only a colorful and diverse bean mixture but also a genetically dynamic and possibly adaptive one.

SUMMARY AND CONCLUSIONS

This thesis has documented the variability in 15 bean landraces and has attempted to address the question: "What forces generate and maintain variability in the Malawian bean landraces". A summary of the salient findings follows.

1. A low level of outcrossing (1 - 2%) was found in experimental plots in the central region of Malawi. Many lines collected from the northern region were found to be segregating and it is likely that outcrossing in this region is as high or higher than that observed in the experimental plots.

2. Seven bee species, from three genera, were observed visiting bean flowers. The same species are known to effect pollination in pigeon peas in Kenya and it is likely that they are the primary pollinators of beans in Malawi.

3. The segregation of a single heterozygous seed collected in the northern region was documented. Over 60 unique seed types were recovered. It is clear that even a single outcross may generate a tremendous diversity of seed types in a landrace.

4. The Malawian bean landraces are composed of many lines which are often extremely diverse for phenological, morphological, agronomical and qualitative traits.

5. It was hypothesized that variability in phenological traits, by extending critical growth phases for the landrace as a whole, lessens the risk of crop loss to the farmer.

6. The fact that both determinate and indeterminate beans coexist in these landraces is seen as an indication that very little intraspecific competition occurs within a Malawian bean landrace. Rather, as beans and maize are generally grown in association, the primary competition confronting beans is that against maize.

7. The fact that bean plant populations are very low in Malawian fields was suggested as a possible reason that mixtures containing components of various competitive abilities are able to persist.

8. The principal component analysis revealed a north - south clinal pattern in the 15 landraces. This cline appeared to be attributable to the sharp differences observed in flowering and maturing times for the beans from these two zones.

9. The principal component analysis resulting in between-area distances indicated that geographical proximity was unrelated to the distance between landraces based on 21 quantitaive traits.

10. Many statistically significant correlations were observed between environmental variables and plant characters. Several phenological traits were associated with latitude, indicating a possible photoperiodic adaptation. Numerous negative correlations between soil potassium and morphological traits suggest that this nutrient may be exerting a selective force on the morphology of the landraces.

11. The PC distances between lines ranged from 0.0749 to 1.3215. The distance between two closely related Michigan linse, Domino and Black Magic, was 0.2595. It was suggested that lines separated by distances as low as 0.0749 (site 10, lines 23-25) or 0.0930 (site 11, lines 1-24) probably represent a pure line.

12. Some highly uniform seed classes were found to have statistically significant differences between lines for only a few traits. Although the average distance separating these lines was considerably higher than that suggested as being indicative of a pure line, it was postulated that these too may constitute pure lines.

13. Some uniform seed classes were found to have significant differences for very many traits, and correspondingly higher average PC distances. These classes are very likely not pure lines.

14. It was concluded, based on the analyses of uniform seed classes, that bean researchers in Malawi should not evaluate the relative diversity of a landrace on the basis of seed characteristics alone. Highly uniform seed classes may contain enormous variability for other quantitative traits.

15. The low level of outcrossing present in these landraces was found to have a profound impact on the generation of variability. A continuum of genetic intergradation was observed, progressing from simple mechanical mixtures to hybrid swarms and eventually to very extensive recombination.

16. This genetic intergradation between the original farmer-composited bean lines in a mixture was postulated to result in a fuller exploitation of the environmental niche filled by this species in the maize/bean association.

The Malawian bean landraces represent a vast and unique store of genetic variability which could be utilized by bean researchers throughout the world. To the Malawian farmer this variability probably offers a degree of insurance against crop loss. The recombination occurring in these landraces due to outcrossing, combined with the various selection pressures exerted by the rigorous environment, serves to continually improve the adaptation of these landraces. Thus, the Malawian landraces are genetically dynamic populations which are shaped both by the local people and the environment. The replacement of these complex entities by uniform pure lines should be viewed with great circumspection.

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APPENDIX A

Character measurements and scores
for the 375 Malawian bean lines,
and the 4 Michigan cultivars
included in the study.

Character measurements and scores of the 375 lines collected from 15 farm sites in the northern region of Malawi.

```
0   1 AREA
43   2 SITE CODE
42   3 TREATMENT CODE
26   4 Days to emergence
27   4 Days to first flower
28   5 Days to end of flowering
35   4 Flowering duration
34   5 Days to physiolog. maturity
22   4 LEAFLET AREA CM SQ
6   3 LEAFLET LENGTH
7   2 LEAFLET WIDTH
31   3 LEAF SHAPE RATIO
24   2 PETIOLE LENGTH
14   2 HYPOCOTYL LENGTH
23   3 SEEDLING DRY WEIGHT AT THREE WEEKS  GMS.
13   3 HYPOCOTYL DIAMETER
21   3 NODES ON MAIN STEM  (AT PHYSIOLOGICAL MATURITY)
19   2 SEED LENGTH
20   1 SEED WIDTH
37   3 SINGLE SEED WEIGHT
40   3 NUMBER OF SEEDS PER POD
41   4 PODS PER PLANT
38   5 YIELD PER PLANT GMS
39   5 NUMBER OF SEEDS PER PLANT   FECUNDITY
17   2 SEED PRIMARY COLOR
18   2 SEED SECONDARY COLOR
16   1 SEED PATTERN
10   1 COLOR OF BANNER
11   1 COLOR OF WINGS
12   1 GROWTH HABIT

CASE 0  4   4    2    2     2    3     3    2   0  0   3  2  1   2   1   2  1 2   3   4    4     3     3 1  1 1 1 1 1
 NO. 0  3   2    6    7     8    5     4    2   6  7   1  4  4   3   3   1  9 0   7   0    1     8     9 7  8 6 0 1 2
--------------------------------------------------------------------------------------------------------------------
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1202 1  1   2 1200 4600  6633 2033  9133 6157 130 79 163 68 70 111  77 165 18 8 462 484 2312  5162  1119 6 14 4 2 1 2
1203 1  1   3 1200 4533  7033 2500  9400 4674 103 71 145 66 72 160  87 175 16 7 530 376 3769  7480  1416 2  0 0 4 3 2
1204 1  1   4 1233 4667  6767 2100  9200 5079 108 68 161 63 68 132  77 115 14 8 453 469 2358  5042  1109 6 14 4 2 1 2
1205 1  1   5 1167 4533  6867 2333  9167 5503 119 70 171 53 78 146  85 175 15 7 422 378 2460  3902   924 5  0 0 4 3 2
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1211 1  1  11 1300 4767  7100 2333  9533 3871  90 67 137 67 68 119  78 155 16 8 429 373 2833  4387  1031 2  0 0 4 3 2
1212 1  1  12 1300 4733  6933 2200  9233 4640  97 68 145 71 77 134  81 185 15 7 498 369 2705  4967   995 2  0 0 4 3 2
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```

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Data file B:pcadatl
Title:  CHARACTER MEASUREMENTS OF PCA LINES

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 NO.  0  3   2    6    7     8    5      4    2   6  7   1  4  4   3    3   1  9 0   7   0    1      8      9  7  8 6 0 1 2
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 1222 1  1  22 1300 4600  7033 2433   9833 4139 102 63 163 63 67  95   82 205 16 8 577 371 3440   7424   1282  2  0 0 4 3 2
 1223 1  1  23 1333 4767  7067 2300   9467 3494  90 59 154 64 67 109   82 170 15 8 532 385 3322   6740   1269  2  0 0 4 3 2
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Data file B:pcadatl
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 1276 2  4  76 1267 5200  7033 1833  9067 3969  96 65 147 50 62  97   76 155 14 6 362 420 3921   5947   1642  5   0 0 4 3 2
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 1287 2  4  87 1100 5667  7167 1500  9733 3063  80 56 142 47 66  81   71 215 11 7 270 513 4063   5539   2060  7   0 0 1 1 2
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Data file B:pcadatl
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  1485 4 12 285 1933 6233   8000 1767 10567 3285  83 56 150 44 53 118   67 220 14 6 302 440 2982    4010    1323  3  0 0 4 4 2
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  1500 4 12 300 1267 5667   7567 1900  9733 5637 122 75 165 66 78 109   78 180 17 8 435 469 2104    4319     986 14  0 0 5 4 2
  1501 5 13 301 1200 5600   7467 1867 10000 6828 140 77 182 49 75 133   91 155 15 7 521 527 2489    6792    1310  7  3 8 4 3 2
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  1503 5 13 303 1267 5467   7100 1633  9967 5256 118 70 173 65 73 133   89 195 15 8 550 487 2775    7365    1333  9  0 0 4 3 2
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  1506 5 13 306 1267 5267   6933 1667  9633 4104 111 57 193 58 61  99   75 123 18 8 461 422 2477    4859    1038  3  0 0 4 3 2
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Data file B:pcadatl
Title:  CHARACTER MEASUREMENTS OF PCA LINES

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 1526 5 14 326 1167 5200  7400 2200  9400 4563 102 71 146 43 66 119   82 115 13 6 335 558 2624  4888  1462  3  0 0 5 4 2
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Data file B:pcadatl
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<u>Michigan lines included in the P.C.A. study.</u>

1576 = Domino

1577 = Black Magic

1578 = Swan Valley

1579 = Seafarer

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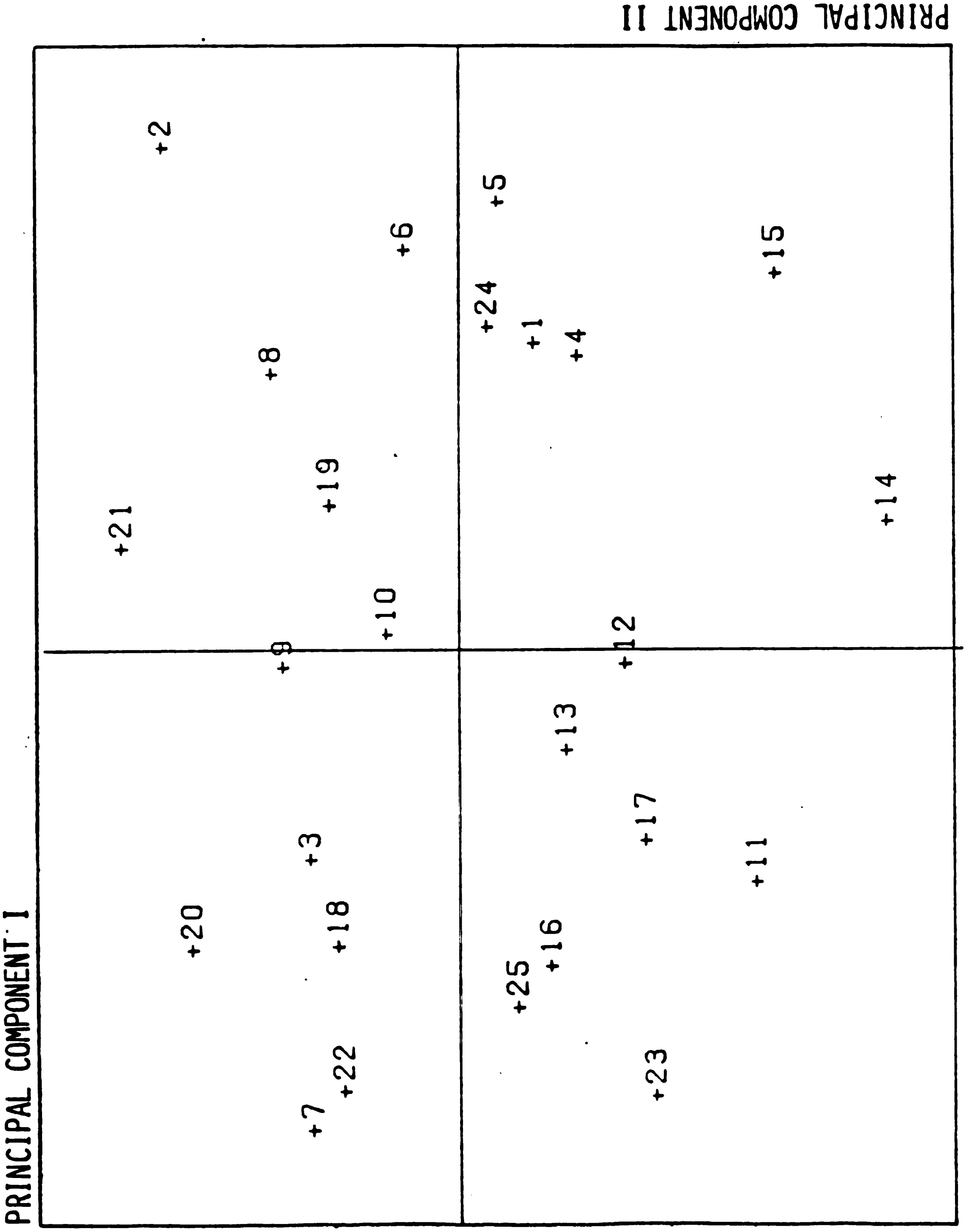
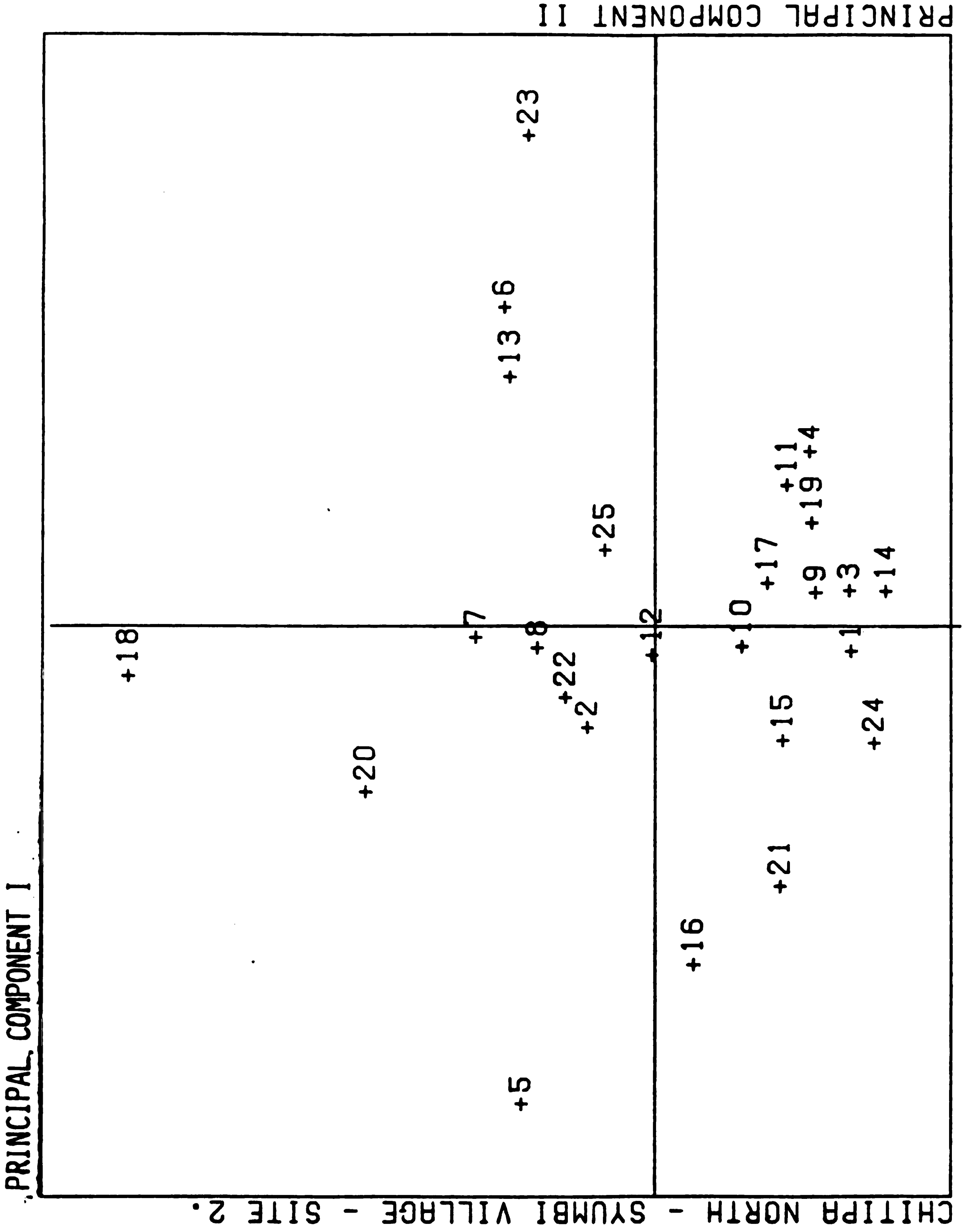
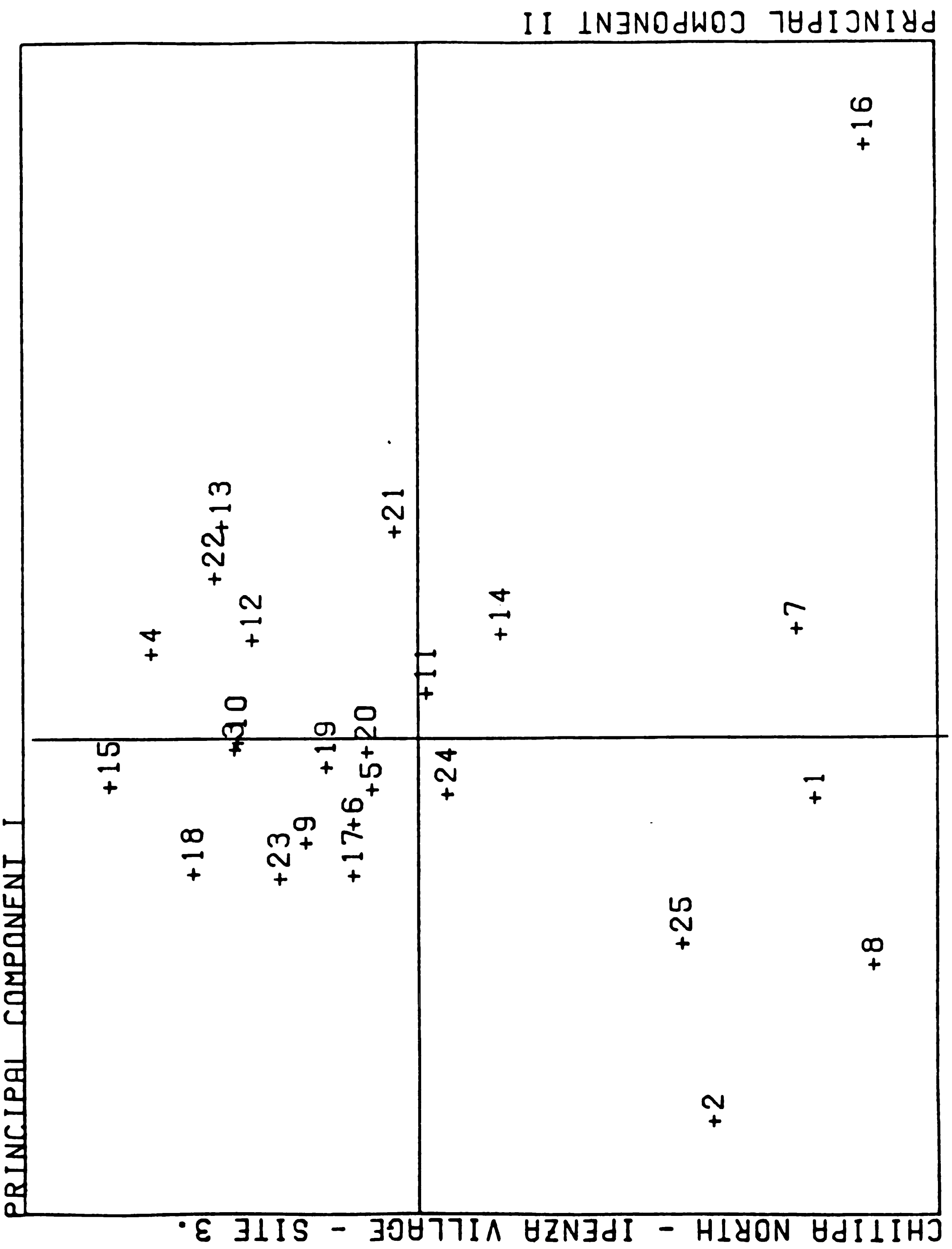
APPENDIX B

Plots of principal components I and II
for the 15 collection sites.



CHITIPA NORTH - MWENELOZA VILLAGE - SITE 1.


PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I
CHITIPA NORTH - SYUMBI VILLAGE - SITE 2.
+23
+13
+6
+25
+11
+4
+19
+17
+9
+3
+14
+18
+7
+8
+12
+10
+1
+22
+2
+15
+24
+20
+21
+16
+5


CHITIPA NORTH - IPENZA VILLAGE - SITE 3.
PRINCIPAL COMPONENT I
PRINCIPAL COMPONENT II
+1
+2
+4
+5
+6
+7
+8
+9
+10
+11
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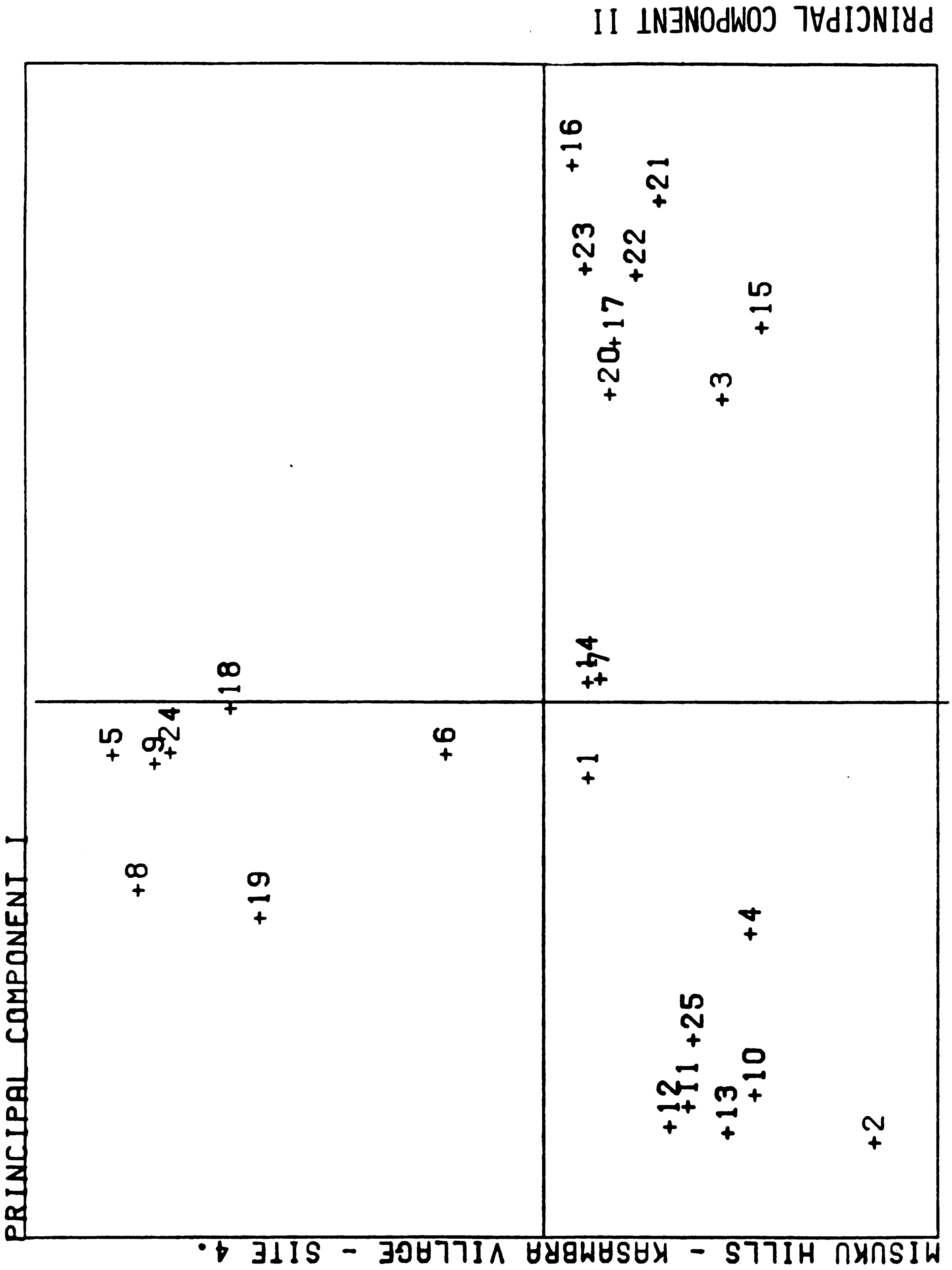
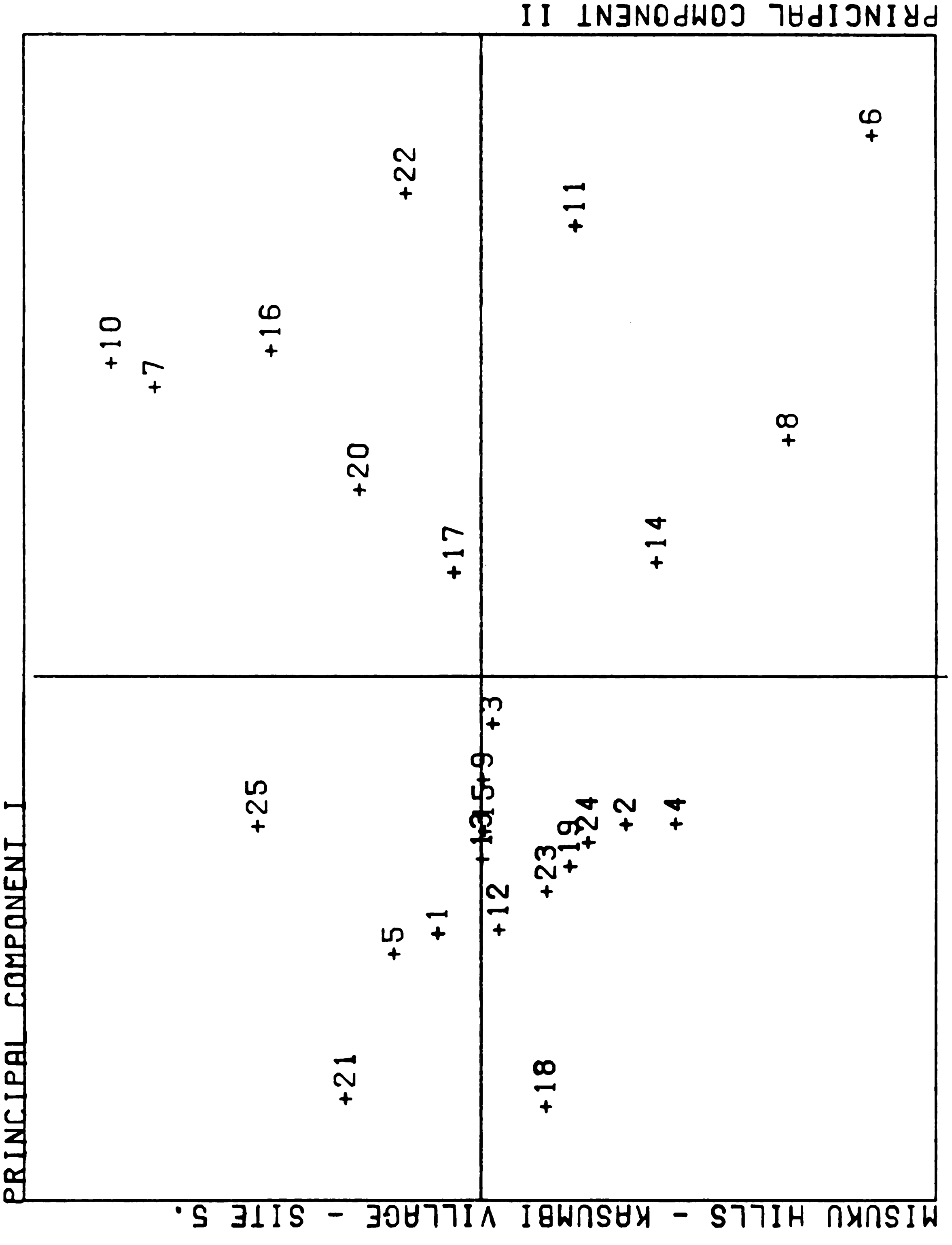
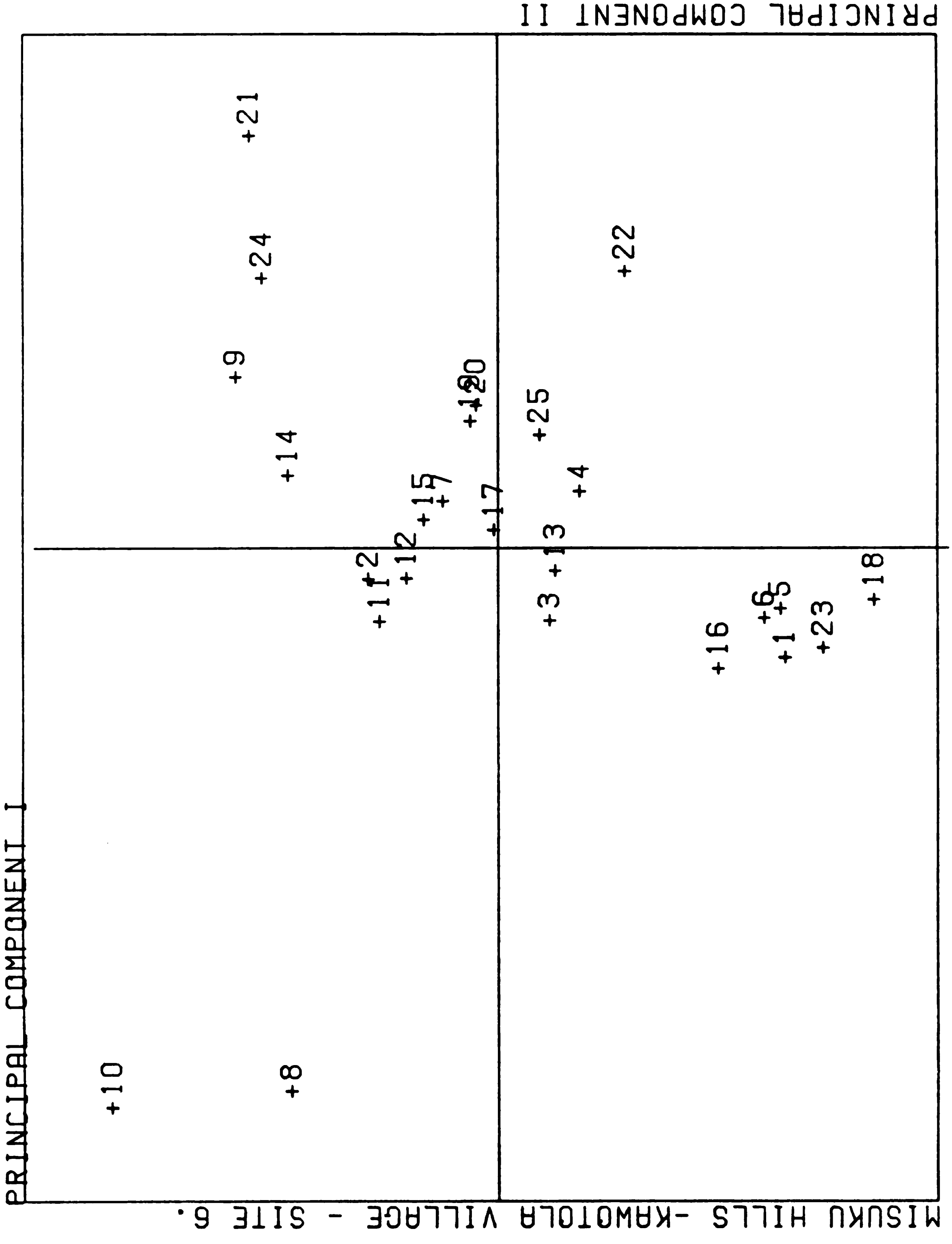
+22
+23
+24
+25

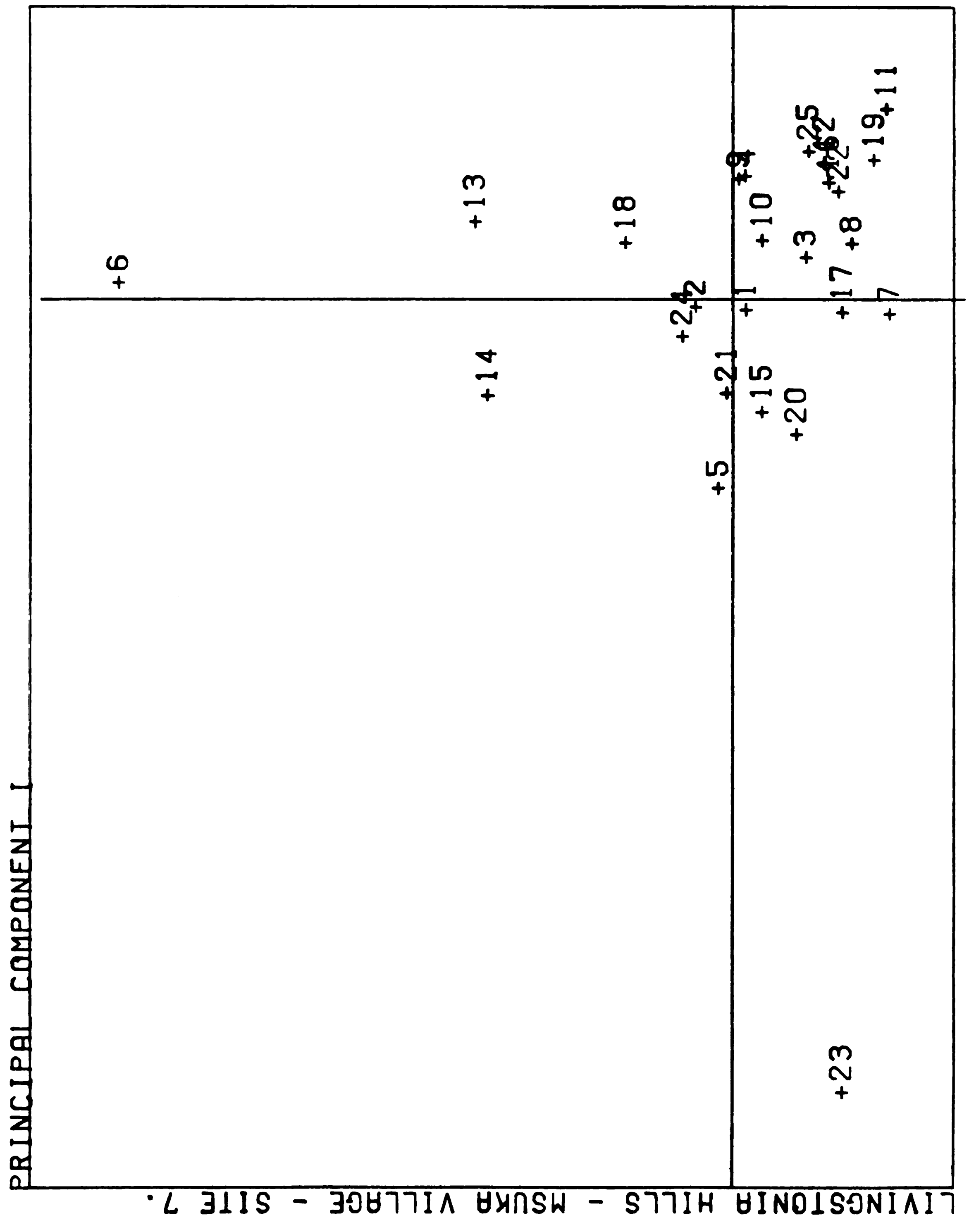

PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I
MISUKU HILLS - KASAMBRA VILLAGE - SITE 4.
+16
+21
+23
+22
+15
+17
+20
+3
+14
+7
+18
+5
+9
+24
+6
+1
+8
+19
+4
+25
+11
+12
+10
+13
+2

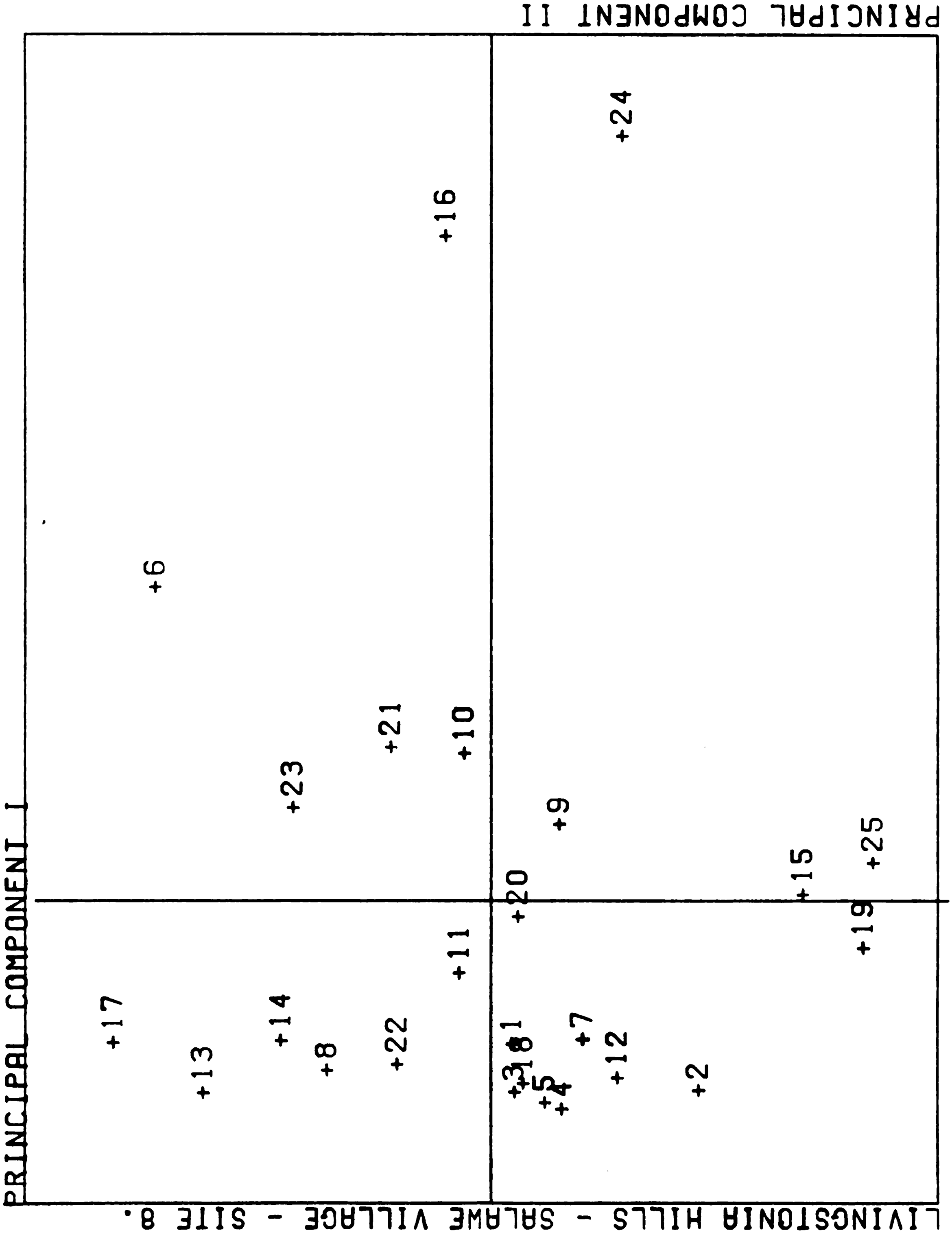


MISUKU HILLS - KASUMBI VILLAGE - SITE 5.



MISUKU HILLS -KAWOTOLA VILLAGE - SITE 6.


PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I
LIVINGSTONIA HILLS - MSUKA VILLAGE - SITE 7.
+6
+13
+18
+14
+24
+2
+21
+5
+1
+9
+4
+10
+3
+15
+20
+17
+8
+7
+25
+22
+19
+11
+23


PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I
LIVINGSTONIA HILLS - SALAWE VILLAGE - SITE 8.
+1
+2
+3
+4
+5
+6
+7
+8
+9
+10
+11
+12
+13
+14
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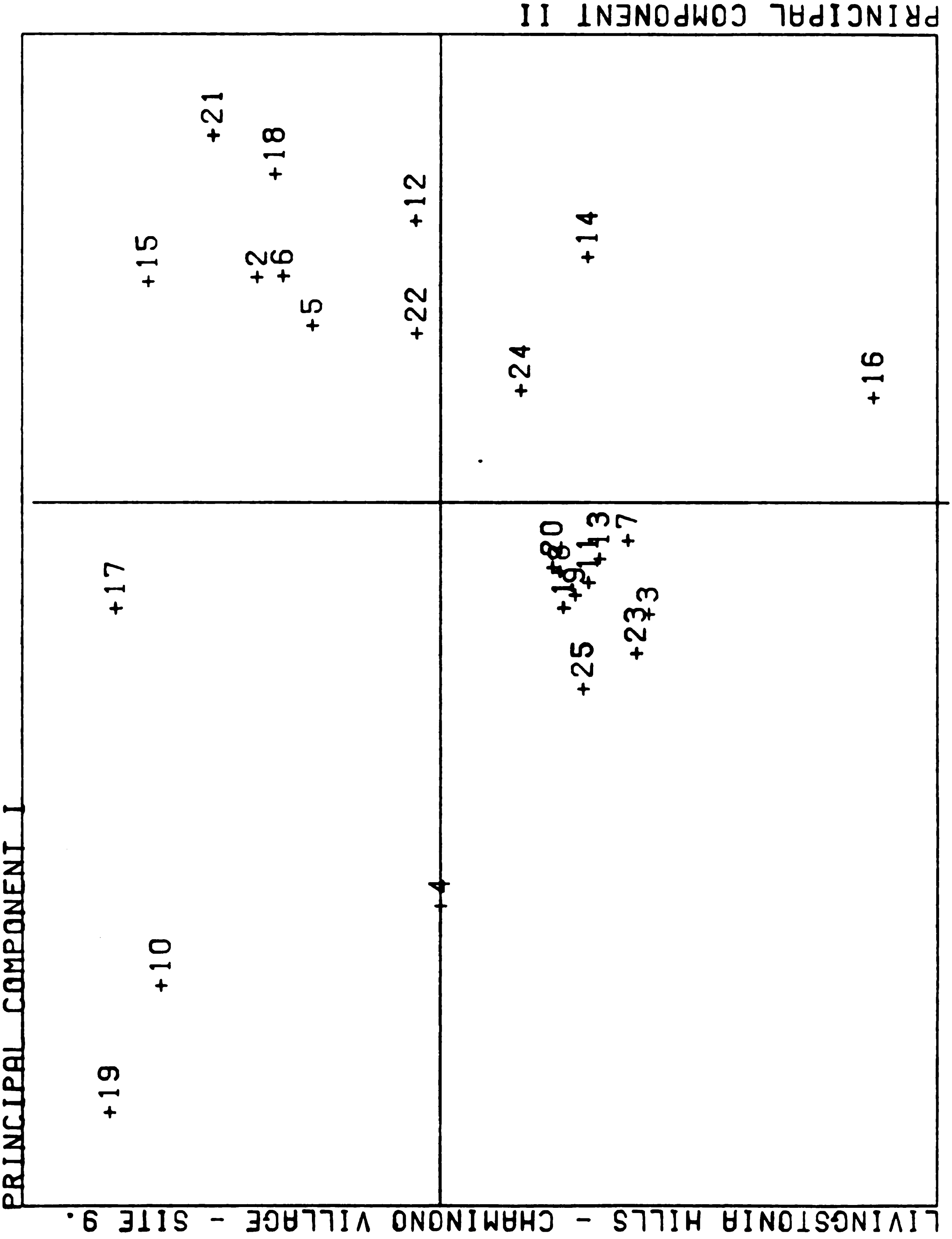
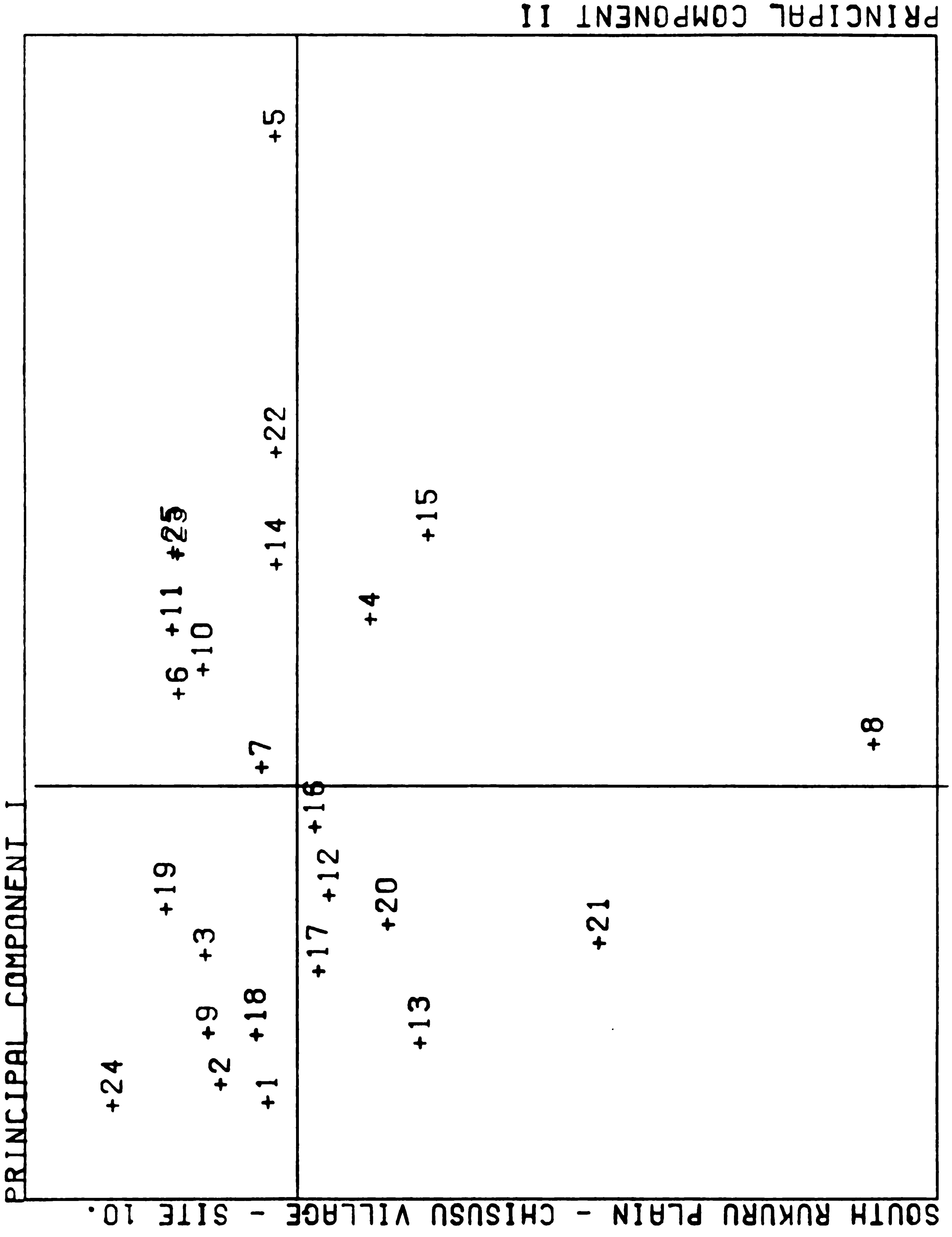
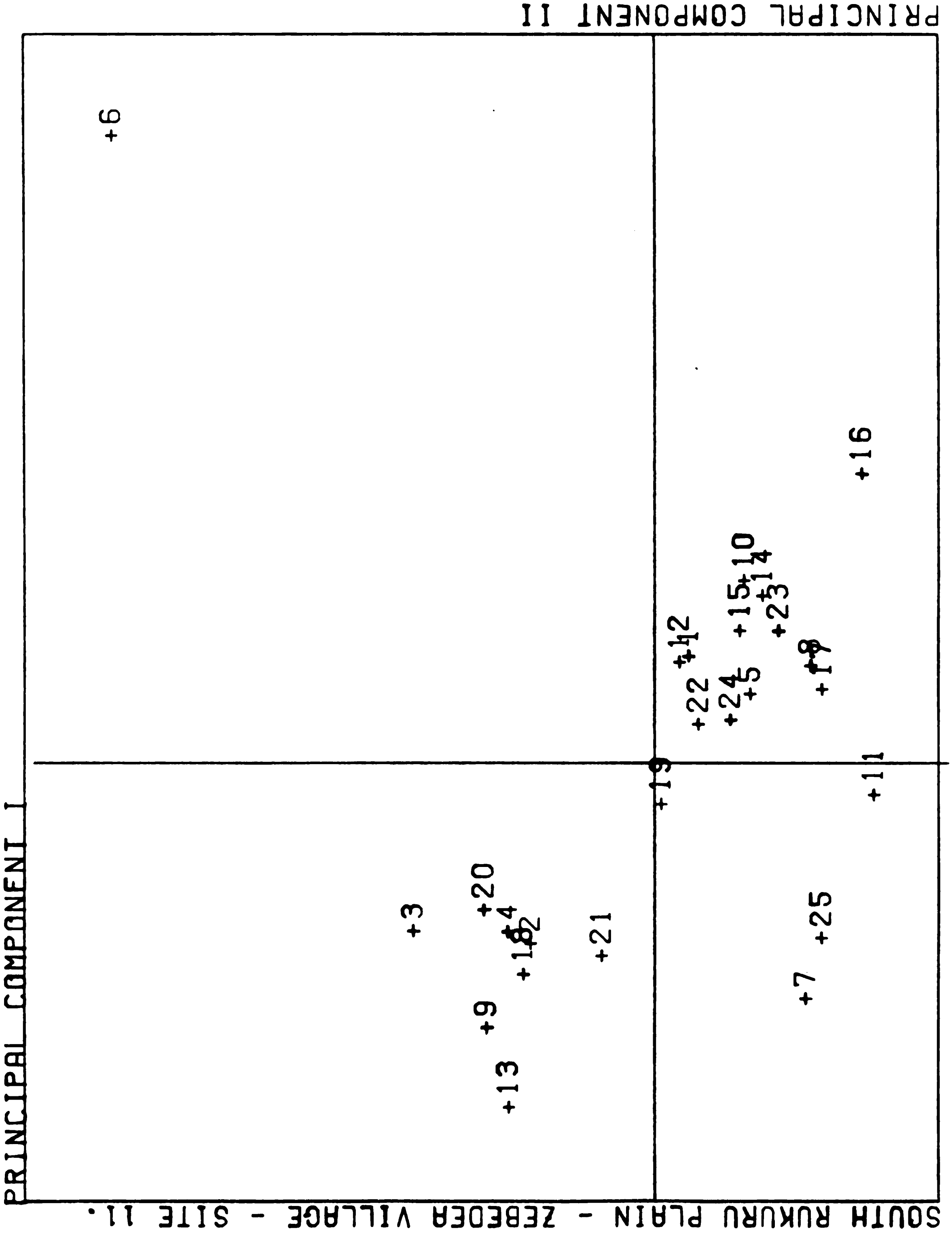
+22
+23
+24
+25

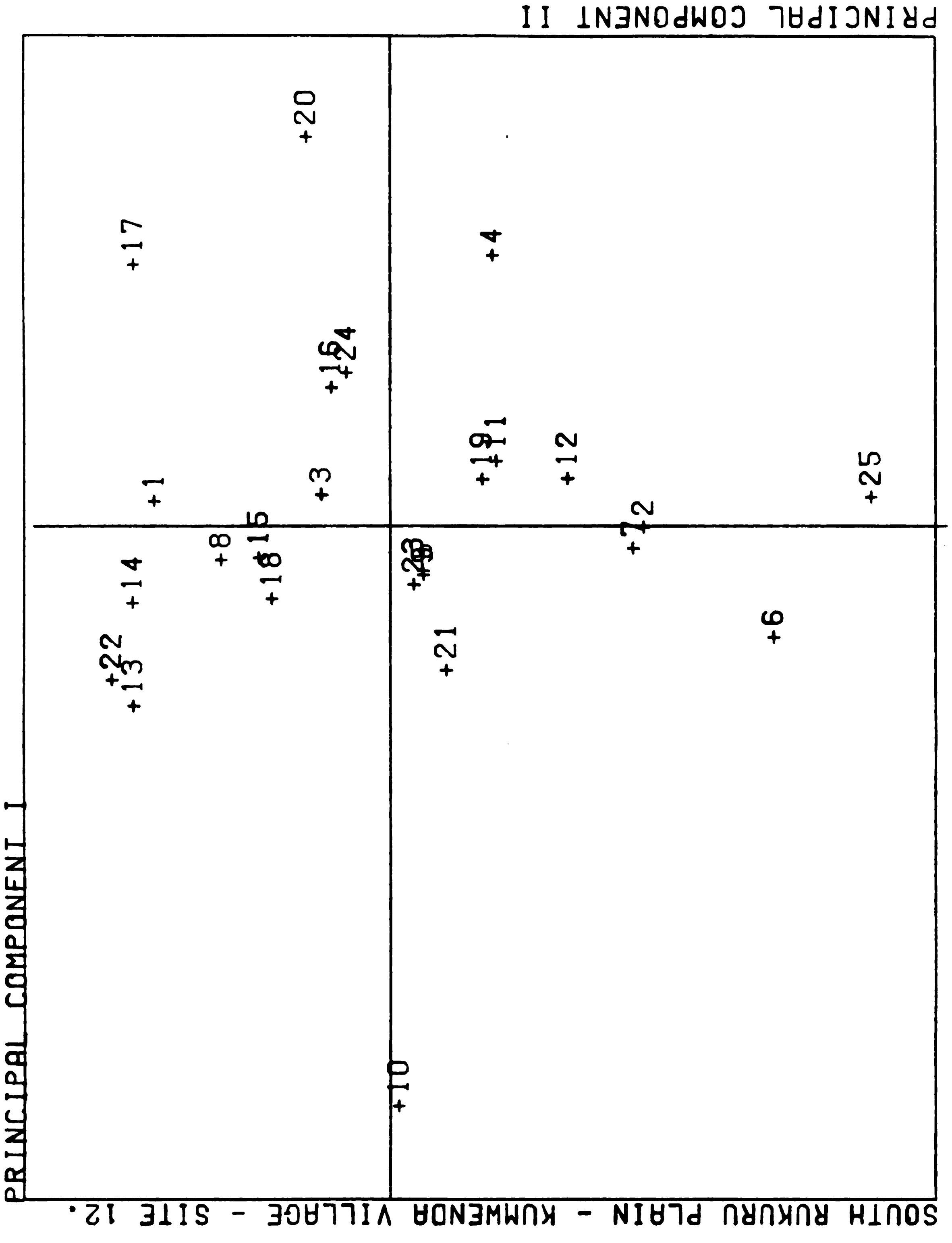

PRINCIPAL COMPONENT II
PRINCIPAL COMPONENT I
LIVINGSTONIA HILLS - CHAMINONO VILLAGE - SITE 9.
+21
+18
+12
+15
+2
+6
+14
+5
+22
+24
+16
+20
+8
+13
+7
+1
+9
+11
+3
+23
+17
+25
+4
+10
+19

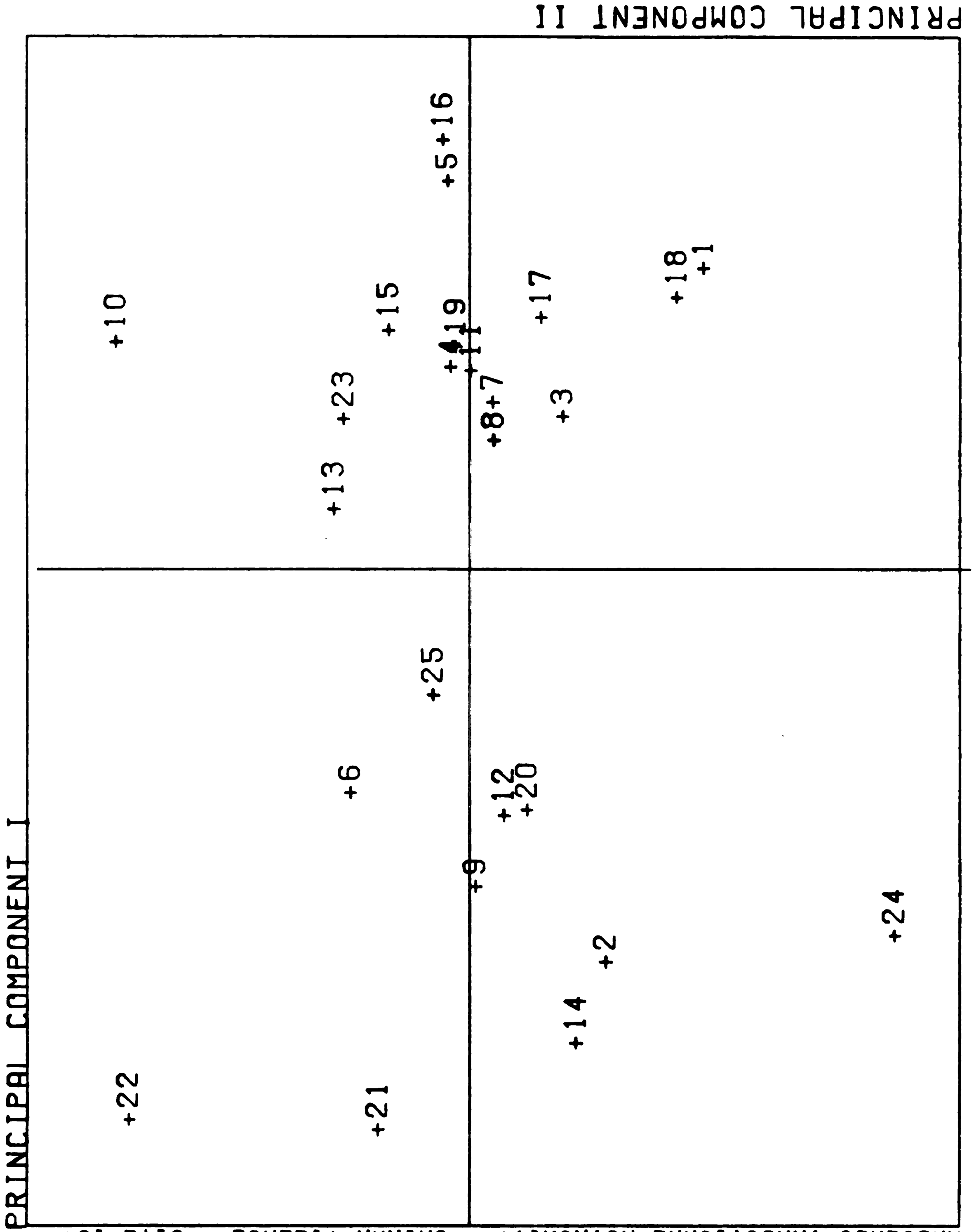


SOUTH RUKURU PLAIN - CHISUSU VILLAGE - SITE 10.

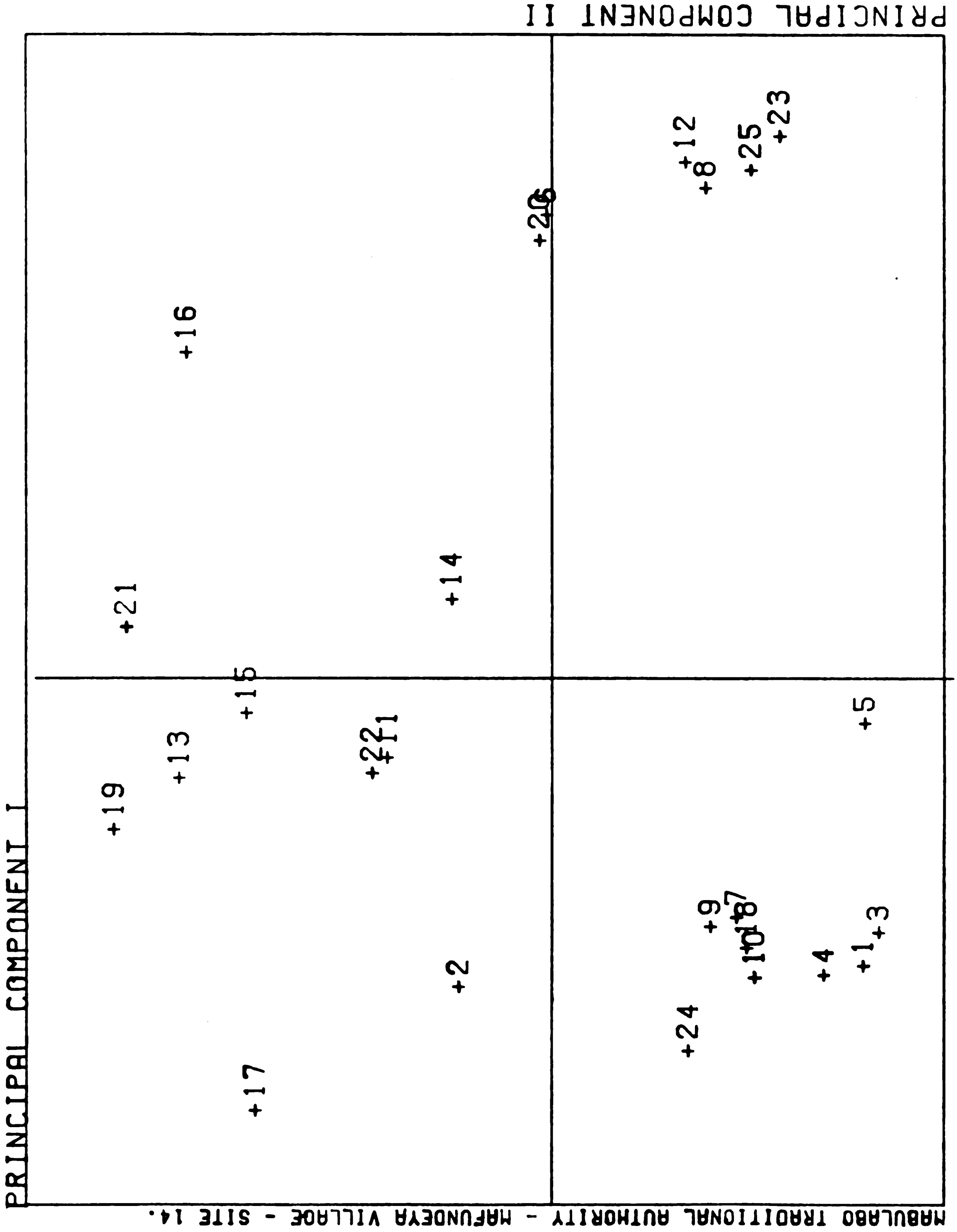


SOUTH RUKURU PLAIN - ZEBEDEA VILLAGE - SITE 11.

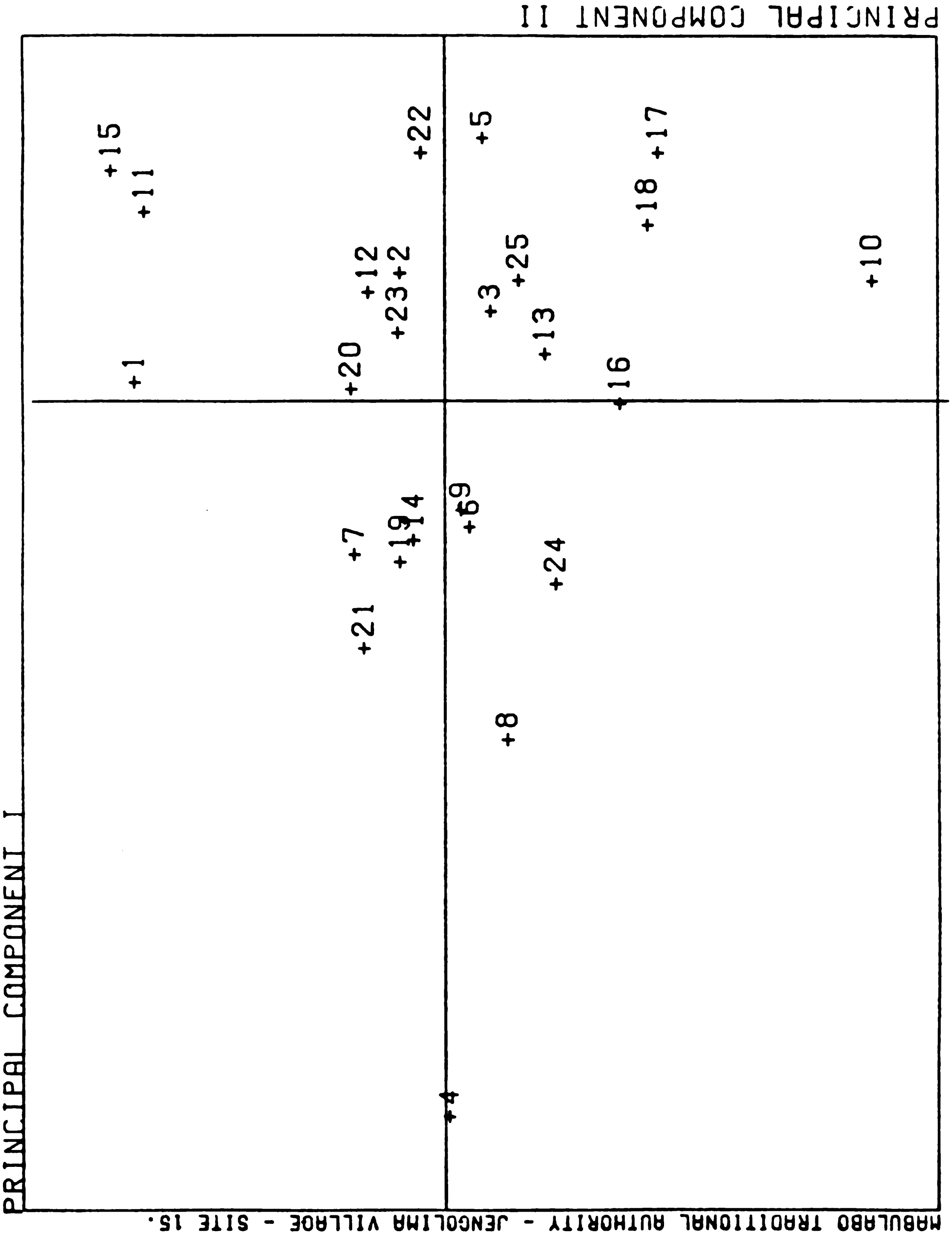

SOUTH RUKURU PLAIN - KUMWENDA VILLAGE - SITE 12.



MABULABO TRADITIONAL AUTHORITY - CHIRWA VILLAGE - SITE 13.



MABULABO TRADITIONAL AUTHORITY - MAFUNDEYA VILLAGE - SITE 14.



MABULABO TRADITIONAL AUTHORITY - JENGOLIMA VILLAGE - SITE 15.