BREEDING SYSTEM, GENETIC VARIABILITY, AND RESPONSE TO SELECTION IN *PLECTRITIS* (VALERIANACEAE)

by

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Abstract

Plectritis congesta and P. brachystemon are two very closely related species which grow sympatrically, and differ in their breeding system, some associated morphological (floral) characters, and isozyme phenotypes. Plectritis congesta is approximately 70% outcrossed in nature, while P. brachystemon is less than 3% outcrossed in natural populations. Theory would predict that, all other things being equal, the outcrossed species would be more variable genetically than the selfed species. Since selection acts on genetic variability, the two species could be expected to respond differently to it. Six generations of plants of both species were grown under controlled conditions, and measured for a number of characters. Control and treatment (selection for tall and short height, and for early and late anthesis) populations were maintained. Two sets of P. congesta populations were maintained, one outcrossed (approximately 65%) and one selfed (outcrossed approximately 15%); the P. brachystemon populations were naturally self-pollinating. Selection pressure in the experiment was approximately 90%; 20 of the 200 plants in any population were selected to form the next generation, on the basis of height or flowering time in the treatment populations, and at random in the control populations.

The P. congesta populations responded to divergent selection for height at anthesis, indicating that genetic variability for this character was present in the populations. The outcrossed lines, PCO, diverged 66% or 148 mm from the control line; the selfed lines, PCS, diverged 78% or 175 mm. There were no significant differences between the outcrossed and selfed P. congesta lines over the course of the experiment. Two estimates of narrow sense heritability - realised heritability (b_c) and parent-offspring regression (h^2) - quantified this genetic variability: in PCO b_c = 0.53,

$h^2 = 0.45$; in PCS $b_c = 0.58$, $h^2 = 0.44$. There was a decline in the phenotypic variance for height at anthesis in the P. congesta lines selected for this character. In contrast, the P. brachystemon populations did not respond to selection for height at anthesis, and appear to have no detectable genetic variability for this character.

Both species appear to have significant genetic variability for flowering time, as both responded to divergent selection for this character. The PCO lines diverged 33.5% or 31.8 days from the control line, the PCS lines diverged 28.7% or 27.3 days, and the P. brachystemon lines, PBS, diverged 18.5% or 21.5 days. According to the heritability estimates, P. congesta is more variable genetically: in the PCO lines $b_c = 0.77$, $h^2 = 0.60$; in PCS $b_c = 0.75$, $h^2 = 0.72$; while in PBS $b_c = 0.49$, and $h^2 = 0.42$. There was a decline in the phenotypic variance for flowering time in all three species groups.

Of the other measured but unselected characters - number of days to emergence, number of nodes at anthesis, number of primary branches at anthesis, and fruit production - some responded to the selection pressure with divergence, notably those characters which were correlated with the selected characters (for example, number of nodes at anthesis, correlated with flowering time). With others there was no change which could be attributed to the selection procedure.

There was no evidence from two qualitative characters - fruit wing phenotype and fruit pubescence pattern phenotype - for any response to selection; dispersion in both characters was not significantly different from that expected to result from random drift. The relatively high increase in aberrant characters in the P. congesta lines compared to the P. brachystemon lines is probably indicative of inbreeding depression in the normally outcrossed P. congesta.

It appears that despite the difference in breeding system, the two Plectritis species are able to maintain variability by similar processes (genetic) in some characters, as in flowering time, and by different processes (genetic in P. congesta, phenotypic in P. brachystemon) in other characters, as in height at anthesis.

Thus one quantitative character, height at anthesis, follows the pattern predicted by the breeding system difference, with the outcrossed P. congesta being much more variable genetically than the selfed P. brachystemon. This agrees with the levels of variability observed by Layton (1980) in electrophoretically detectable isozymes, and observed by Ganders and Maze (unpublished) in metrical fruit characters.

The other quantitative character, flowering time, shows considerable genetic variance in the populations of the selfed P. brachystemon, though less than in the populations of P. congesta. The maintenance of such relatively high levels of genetic variability in the face of the strong inbreeding pressures which must be present in P. brachystemon populations is certainly adaptive, and probably comes about through occasional outcrossing and multiniche selection for variability among the segregating lines.

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Breeding system, genetic variability, and response to selection in *Plectritis* (Valerianaceae).

Introduction

Genetic variability in various organisms has been a major object of study since the rediscovery of Mendel's laws of inheritance and their synthesis with Darwin's theory of evolution by natural selection. The kind of questions to which answers are sought include questions about the extent to which variability is present in individuals, populations, or taxa; about the ways in which variability is generated, maintained, or lost; and about the effect which variability may have on the fitness or survival of an individual, population, or taxon.

This study deals with the following questions about genetic variability. First, how has the amount of genetic variability underlying the expression of quantitatively inherited characters in a population of plants been affected by the breeding system of that population? Second, if the breeding system has affected the amount or nature of genetic variability, can this effect be detected by observing the response to selection in two taxa between which the major biological difference is in their breeding system? Finally, how does the genetic variability present in quantitatively inherited characters compare to that of other (monogenic) characters, both within and between taxa with different breeding systems? To combine the questions in more concrete terms, is a population of inbreeding plants more or less variable genetically than a population of "otherwise identical" outbreeding plants with respect to quantitatively inherited characters, does it respond more or less quickly to selection pressures on these

characters, and does the genetic variability in multigenic characters follow the same patterns as variability in monogenic characters?

Both theoretical predictions and experimental evidence have provided some answers to all three of these questions. Differences in genetic variability between plant species of varied breeding systems have been studied by population biologists; in most cases the characters studied have been monogenic rather than quantitatively inherited. Differences in response to selection are of vital interest to plant breeders; in most of their studies the goals have not included assessing the effects of the breeding systems of the plants involved, or more particularly comparing species of differing breeding system. There is a place (not to say a gap) to be filled by selection studies of quantitatively inherited characters in natural populations; it is to be hoped that such studies will add to what is known about breeding systems, genetic variability, response to selection, and the interactions among the three.

Breeding system and genetic variability

Theoretical considerations

A first step in answering questions about genetic variability is necessarily the definition of some of the terms. Genetic variability is a broad term which can lead to some confusion if loosely applied. It encompasses a number of parameters in any population, including the numbers and frequencies of alleles at various gene loci, the numbers and frequencies of various genotypes, and the distribution of genotypic components of the total phenotypic variance for various characters. Although these parameters are not independent, they can be divided into two groups on the basis of

whether or not they are subject to selection directly. The first group I will call the potential components of the genetic variability in a population. In the simplest genetic sense, a gene locus is variable (polymorphic) if more than one allele occurs at it. For any population the number and frequencies of alleles at various loci can theoretically be observed. These alleles will be combined to form the genotype of an individual. The number and frequencies of various genotypes in any population can also be observed theoretically. Various indices can be derived from these types of observations; some examples which are commonly used in studies of real populations are the number or percentage of loci which are observed to be polymorphic, and the number of alleles per polymorphic locus. In addition, the frequencies of genotypes expected in a population behaving according to particular assumptions can be calculated. Most often the assumptions are those leading to Hardy-Weinberg equilibrium in a theoretical population. The populations under study may not be behaving according to the assumptions by which the genotype frequencies have been derived. For example, if at a particular locus a population has two alleles, A_1 and A_2, then theoretically there are three genotypes possible. An actual population may in fact be missing any one of the three genotypes (or even both homozygous genotypes), and be less variable in fact than it appears in theory. Many studies of this type of genetic variability calculate genotype frequencies rather than observing them in populations. Since alleles and genotypes are not selected directly but rather through their expression in phenotypes, it should be kept in mind that indices which compare populations on this basis may not be assessing the genetic variability available for selection. This has been a particular problem in studies dealing with isoenzymes; the selective values of

particular isoenzyme phenotypes are for the most part unknown. I will refer to these estimates of potential genetic variability as estimates of genetic diversity (a term which has a more specific application in some of the literature of population genetics).

If the contribution of various genotypes to the genotypic component of the total phenotypic variance for a particular character can be assigned arbitrarily or determined by experiment, then one is dealing with the second group of parameters, which I will call the realised components of the genetic variability. For any character a particular phenotype can be assigned a numerical value, be it a fitness value or an actual measurement (height, weight, etc.), and the distribution of these values in a population will have a mean and a variance. The genotypic component of this total phenotypic variance is referred to as the genetic variance, and it is upon this variance that selection may act.

The effect of breeding system on the potential genetic variability, or genetic diversity, can be predicted in theory if a number of assumptions are invoked. If two populations are initially identical in all respects, that is, contain equal numbers and frequencies of genotypes, and are otherwise in Hardy-Weinberg equilibrium, then breeding system differences will affect them in the following way. The frequency of heterozygous individuals at a particular locus, and in consequence the total number of genotypes, will quickly decline in the inbreeding or autogamous population compared to the random mating population. However, the total number and frequencies of alleles, the percentage of loci which are polymorphic, and the number of alleles per polymorphic locus will remain the same, as will the genotype frequencies expected under Hardy-Weinberg equilibrium.

If the equilibrium assumptions are relaxed, and realistic and finite

population size and selection are affecting the populations, random drift and selection will reduce the total number of alleles in the selfing population faster than in the outcrossed one, and genetic diversity as measured by the percentage of loci polymorphic, the number of alleles per polymorphic locus, and the expected frequency of heterozygotes at equilibrium will thus be reduced in the selfer relative to the outcrossed population. The degree of difference in genetic diversity between the two populations of different breeding system will depend on the difference in their rates of inbreeding, the effective population size, and rates of selection.

The effect of the breeding system on the realised genetic variability or genetic variance can also be predicted in theory, again subject to a number of simplifying assumptions. If we start with the same two populations as mentioned above, with identical genotypic structure under Hardy-Weinberg equilibrium, then breeding system differences will have the following effects. If the environmental component of the total phenotypic variance in this case is taken to be zero, then the genotypic values are contributing all of the phenotypic variability. With selfing, as heterozygous genotypes are lost from the population the variance of the phenotypic values will increase relative to a random mating population. Thus inbreeding on its own will increase genetic variance.

If we again relax the equilibrium assumptions by assuming realistic finite populations on which selection is acting, then the theoretical prediction becomes rather problematical. The relatively larger loss of alleles due to random drift and selection in finite populations of selfers will tend to reduce the genetic variance. Simultaneously, inbreeding will increase the genetic variance relative to a random mating population. The

effects on genetic variance of inbreeding and random drift / selection will be in opposite directions, and the net effect cannot be generalized. Lande (1977) has proposed a model which indicates that if the populations are large (infinite), but with selection and mutation acting, then the breeding system will have no effect on the amount of additive genetic variance maintained.

To summarize, such theoretical treatments of realistic populations (without extensive simplifying assumptions) as are available should be generalized with caution. Nevertheless, compared to random mating, selfing in finite populations is likely to lead to a loss of genetic diversity, and whether this is accompanied by a net reduction in genetic variance will depend on factors unrelated to the breeding system, such as population size and selection pressures.

Experimental evidence

Variability has been studied in populations of many plant species, both natural and domesticated. Discontinuities in variation patterns between taxa form the basis for taxonomic studies; genetic variability is the source of improvement by plant breeders in economically important species; and the interaction of genetic variation and natural selection is the object of evolutionary studies. Studies specifically isolating breeding system and genetic variability are limited, and comparisons between closely related species differing in breeding system are as yet very few.

The experimental evidence relating breeding system and genetic variability can be divided into two groups in which the estimates of genetic variability roughly parallel those outlined earlier as genetic diversity and genetic variance. The first group consists of evidence from monogenic or

single locus traits, whose qualitative nature makes assignment of specific phenotypic values, and thus population parameters such as mean value and variance, difficult. In some cases fitness values have been estimated experimentally, but for the most part the experimental evidence is in the form of estimates of genetic diversity such as allele and genotype frequencies, and indices such as the percentage of loci polymorphic and number of alleles per polymorphic locus. The second group consists of evidence from characters which are known or assumed to be multigenic, or quantitatively inherited. For these characters the estimates are approximately estimates of genetic variance, although as will be seen they may require fairly elaborate experimental designs to eliminate environmental components of the variance and obtain more exact estimates of the genetic variance.

Monogenic traits

Because of the ease with which relatively large numbers of characters can be studied, the bulk of studies allowing a comparison of breeding system and genetic variability in monogenic characters involve electrophoretically detectable enzyme variation. Hamrick et al. (1979) have reviewed the isozyme data recently, relating levels of electrophoretic variation (genetic diversity) and life history characteristics in a large number of plant species. They report that for three indices of diversity - percentage of loci polymorphic, number of alleles per polymorphic locus, and a polymorphic index (frequency of heterozygotes expected under Hardy-Weinberg equilibrium) - 36 primarily outcrossed species showed more diversity than 33 primarily selfed species. For the most part these data combine

relatively unrelated taxa in each breeding system group, but there are some comparisons which may be noted. For example, groups of congeneric species in which levels of genetic diversity have been confirmed to be higher in the outcrossed species than in the selfed species include: Limnanthes alba (outcrossed) and L. floccosa (selfed) (Brown and Jain, 1979); Clarkia rubicunda, C. amoena (outcrossed), and C. franciscana (selfed) (Gottlieb, 1973); Gaura suffulta (outcrossed) and G. triangulata (selfed) (Levin, 1975); Phlox drummondii, P. roemariana (outcrossed), and P. cuspidata (selfed) (Levin, 1978); Leavenworthia alabamica, L. crassa, L. stylosa (outcrossed), L. uniflora, L. exigua, and L. torulosa (selfed) (Solbrig, 1972); Lycopersicon pimpinellifolium (outcrossed) (Rick et al., 1977) and L. parviflorum (selfed) (Rick and Fobes, 1975). At the conspecific level, populations of Lycopersicon pimpinellifolium vary in breeding system from relatively outcrossed to relatively selfed, and the more highly outcrossed populations have higher levels of genetic diversity (Rick et al., 1977). In Oenothera, Ellstrand and Levin (1980) found that there was a significant difference in gene diversity between the more diverse, outcrossed O. grandis and the selfed O. mexicana. A third species, O. laciniata, which is highly inbred but a permanent translocation heterozygote, has relatively high diversity, not significantly different from O. grandis. Of particular interest is the study of the two closely related species Plectritis congesta and P. brachystemon, which indicated that the outcrossed P. congesta has much higher levels of genetic diversity as indicated by isozyme data than the selfed P. brachystemon (Layton, 1980).

There are fewer studies of other types of monogenic characters, particularly in closely related taxa of different breeding systems. Jain and Marshall (1967) found that Avena fatua, which has a slightly higher

outcrossing rate than its relative A. barbata, was polymorphic at three morphologically expressed loci, while A. barbata was monomorphic at the same loci. However, while there is a slight difference in breeding system between them, both Avena species are relatively highly selfed. In outcrossed Plectritis congesta, populations polymorphic for a monogenic fruit wing character are much more common (30 populations polymorphic of 32 studied) than in selfed P. brachystemon (3 of 11 populations) (Ganders et al., 1977b; Carey and Ganders, 1980). In Lycopersicon pimpinellifolium, Rick et al. (1977) found that two monogenic morphological characters showed their highest levels of polymorphism in populations with the highest outcrossing rates and were monomorphic in populations which were relatively highly selfed.

All of the evidence from monogenic traits suggests that selfing reduces the genetic diversity relative to a comparable outcrossed population (most of this evidence comes from isozyme loci, which may or may not be representative of all loci). This is in agreement with the theoretical predictions.

Quantitative traits

Data on the genetic variability of multigenic or quantitative characters in selfed or outcrossed species are less straightforward than those on monogenic traits. First, many of these characters are assumed, rather than known, to be multigenic. They might more accurately be termed metrical or continuously distributed traits. Second, these characters are invariably confounded by an environmental component which may be difficult to remove except in large scale, carefully designed experiments. Third, estimates of genetic variability from these characters are further removed from the genome than those from monogenic characters; that is, allele frequencies,

polymorphic loci, and rates of heterozygosity are rarely discernible directly from measurements of these characters unless extensive genetic study has been done. For these reasons a review which brings together data on various taxa from many studies, such as that of Hamrick et al. (1979) for isozyme data, is not feasible, as there is little assurance that the measurements of genetic variability from a wide variety of metrical characters under different experimental designs can validly be compared. Finally, as with monogenic traits, there have been only a limited number of studies of closely related taxa with different breeding systems. I will examine a few of these at this point. In most cases the variability that has been measured has not been partitioned into genetic and environmental components, and the actual measurements are of phenotypic variance, from which estimates of the genetic variability have been extrapolated. I will refer to it as genetic variability, although one may hope that genetic variance is being estimated approximately.

In some cases no significant difference between taxa with different breeding systems was found. Brown and Jain (1979) studied 15 quantitative characters in Limnanthes alba (outcrossed) and L. floccosa (selfed) and concluded that both the total amount of genetic variability and the partitioning of the variability within the taxa (that is, within and between populations of the taxa) were not significantly different between them. This is in contrast to the situation found in the isozymes in these two species, described above (p.9). Studying the Lupinus nanus group, which included four L. nanus subspecies and two other species with outcrossing rates between 0 and 100%, Harding et al. (1974) found no correlation between the outcrossing rate and the amount of genetic variability (in this case estimated genetic variance) for six quantitative characters. In three

grass species, Festuca microstachys (completely selfed), Avena fatua (highly selfed), and Lolium multiflorum (outcrossed), Kannenberg and Allard (1967) found no difference among the three species in genetic variance for three quantitative characters.

In some cases the more highly outcrossed species appears to be more variable. In Lycopersicon pimpinellifolium Rick et al. (1977) noted that several quantitative characters showed maximum variability in geographic areas which coincided with maximum isozyme diversity and maximum outcrossing rate, and minimum variability in areas with minimum outcrossing rates; these observations were unfortunately not based on actual measurements of the characters concerned. Strid (1970) noted that populations of Nigella degenii, an outcrossed species, showed more variability in flowering time and percentage of good pollen than N. doerfleri, a selfed species, but again no measurements of the characters have been reported. In Stephanomeria exigua ssp. coronaria, an outcrossed species, and its obligately selfed derivative S. malheurensis, Gottlieb (1977) measured 33 quantitative traits and found 90% of them to be more variable in the outcrosser. These data must, however, be viewed keeping in mind that S. malheurensis is a recently evolved taxon whose population genetic structure is probably still extensively subject to phenomena such as the founder effect, which also limit genetic variability. In Avena fatua and A. barbata Jain and Marshall (1967) studied 3 quantitative characters and found more genetic variance in the "outcrossed" A. fatua than in A. barbata, but as noted above, both species are actually highly selfed, and the comparison is less useful in this instance. Rogers(1971) found in Papaver rhoeas (outcrossed), P. dubium, and P. lecoqii (selfed) that the outcrossed species showed more within population variability than between population variability for two quantitative characters, and that the selfed species showed the reverse, that is less

within population variability and more between populations. It is unclear whether the overall variability was greater within the outcrossed than within the selfed species. Baker (1953) studied a similar situation in Armeria, looking at several quantitative characters in A. maritima ssp. maritima (self incompatible) and A. maritima ssp. californica (self compatible but more or less outcrossed) where he found that the former, more highly outcrossed taxon was more variable within than between populations, and the latter, more highly selfed taxon more variable between than within populations. In addition, he found that A. maritima ssp. maritima showed more genetic variability in toto than A. maritima ssp. californica. In Plectritis congesta and P. brachystemon, a study of a number of morphometric fruit characters by Ganders and Maze (unpublished) showed the outcrossed P. congesta to be more variable than the selfed P. brachystemon.

Finally there are cases where the selfed taxon is apparently more variable than its outcrossed relative. Hillel et al. (1973) studied 36 quantitative characters in Triticum speltoides (outcrossed) and T. longissimum (selfed) and concluded that the selfed species showed greater genetic variability within families and within and between populations than the outcrossed species.

The overall impression from the evidence of genetic variability in quantitative characters is that the effect of a particular breeding system is in fact difficult to predict. Since in most of the cases presented here the estimate of genetic variance is not an accurate one, it is possible that differences in the environmental component of the total variance may be affecting the comparison.

Genetic variability and the response to directional selection

Theoretical considerations

Can the response to selection for a particular character be predicted by an independent estimate of genetic variability? Again, as with the first question, it is necessary at the outset to define some terms. Selection is any process in a population which divides those individuals surviving to reproduce from those which do not survive to reproduce in some way other than randomly. Directional selection for a character is the differential survival of individuals whose phenotypic expression for that character is different from the population mean in one direction. Response to selection is fundamentally any change in the genetic structure of a population which can be attributed to selection pressure. Selection acts on phenotypes, but the direct response to selection, if any, takes place in the genotypes in a population. It is because genotypic changes in a population are reflected in the total population phenotype that selection responses can be observed, and in the case of long term selection, that the selection process can continue. These responses are usually observed as changes in population mean and variance for those characters which are quantitatively inherited, or as changes in allele or genotype frequencies for characters whose genotype is directly observable in the phenotype of an individual. Fisher's fundamental theorem of natural selection states that the response to selection for a character in a population is directly proportional to the genetic variance for that character in the population. Of interest at this point is the prediction of response to selection for a character on the basis of estimates of genetic variability in <u>independent</u> characters. This is not possible in theory unless some assumptions are made about the extent to which particular characters are representative of the genome as a whole. We could assume that characters for which we have estimates of genetic variability are completely representative of characters which might be

subject to selection. The success of the prediction in this case will depend once again on whether our estimate is of genetic diversity or of genetic variance. As outlined earlier, estimates of genetic diversity do not necessarily measure variability which is available for selection to act upon, whereas genetic variance estimates do. Even genetic variance estimates neglect the environmental component, which may be so large a component of the total phenotypic variability upon which selection acts directly as to confound any prediction. A rigorous theoretical treatment of the question has not yet been produced. Nevertheless, all other things being equal (rate of selection, population size, breeding system), a population which has more genetic diversity would be expected in general to also have greater genetic variance, and to respond faster to selection than one with less genetic diversity. Similarly, a population which has greater genetic variance in some characters could be predicted to have greater genetic variance in other characters, which when selected would show a greater response.

Experimental evidence

There is ample evidence for response to artificial selection in a broad sense in many organisms. The domestication of hundreds of plant and animal species for human purposes has in almost every case involved changes in what are now the domestic taxa, sometimes to the point where feral relatives are unknown or so different from their domesticated derivatives as to make the origins of the latter extremely difficult to trace. Unfortunately, the selection involved in these, often prehistoric, domestications has not been documented in a manner to make them useful in

this study.

Artificial selection, that is selection under the control of humans, should be considered as two separate kinds of process. The first is an attempt to duplicate the processes of natural selection, usually in order to understand what is going on in nature, and involves selecting individuals by their phenotype in one generation (mass selection), breeding them in some natural mating system, and forming the subsequent generation from their progeny. The second type of artificial selection is economically motivated and aimed at producing particular superior genotypes or populations of genotypes in crop plants and animals in the fastest and most economical way. Individual or mass selection is only one of many selection schemes which may be used, in combination with careful breeding programs, to isolate that portion of the available genetic variability which represents the superior genotype(s). Special breeding techniques (diallel crosses, inbreeding, sib matings, back crosses, etc.) and selection regimes (recurrent selection, progeny testing, etc.) are usually employed to increase selectable variation and speed up selection for economic reasons - artificial selection which approximates natural selection is often a relatively slower process. The two types of artificial selection are not mutually exclusive, that is valuable information about natural selection can be obtained from plant and animal breeding studies, and relatively natural selection schemes may produce economically valuable results in some cases.

To help answer the questions about selection, genetic variability, and breeding system as posed, the evidence we require should ideally come from selection experiments where there is an independent estimate of genetic variability for the organism, where the organism studied has a known breeding system, and where the initial populations under selection have not been

bred to change their natural levels of variability, for example by inbreeding an outcrossed species or crossing a selfed species. In addition, for the purposes of comparison to the study undertaken here, the selection method should be comparable (mass selection).

I have been able to find only one experiment where selection for a character has been performed on two taxa for which estimates of genetic diversity or variance from an independent source are available. Jain and Marshall (1970) selected for two extremes of heading date and seed size in Avena fatua and A. barbata. These are two species for which measurements of genetic diversity from isozymes (Marshall and Jain, 1969) and genetic variance in other characters (Jain and Marshall, 1967) are available, and in both cases A. fatua has been shown to be the more variable species. A. fatua responded better to selection for both characters, and this result agrees with the prediction based on the independent estimate of genetic variability. Selection response is sufficiently ubiquitous that careful comparisons such as this are the only ones of real value in answering this question.

Breeding system and the response to selection

Theoretical considerations

Can the response to selection for a particular character be predicted by the breeding system of the organism being selected? Breeding system can only affect the response to selection through its effect on the genetic variance present in the population. As we have seen in the discussion outlined earlier, the effect of breeding system on genetic variance is difficult to predict in theory, but the evidence indicates that selfed taxa contain less genetic diversity than outcrossed taxa. The evidence for

differences in genetic variance between populations with different breeding systems is equivocal.

Inbreeding in an infinitely large population will increase the genetic variance relative to an outcrossed population, and response to directional selection will thus theoretically be faster initially. However, genetic variance will theoretically be depleted more quickly in the inbred population, and selection response will cease earlier (the selection limit having been reached). If in a finite population the selection pressure is heavy enough, it is possible that the selection limit may be farther from the mean of the original population in an outcrossed population than in an inbred one, as loss of alleles through homozygosis and random drift in the inbreeder in early generations may prevent selection of the optimal genotype.

Experimental evidence

The evidence required to distinguish the effect of breeding systems on the response to selection should ideally come from the same type of experiments as outlined earlier under genetic variability and response to selection (p. 15). The available evidence comes mostly from plant breeding studies, and has the attendant shortcomings in this context. Most of the "populations" being selected are not representative of a natural population in terms of levels of genetic variability; that is, even species which have an outcrossed breeding system have usually been inbred, often highly inbred, and naturally selfed species may have been outcrossed a number of ways to increase variability. Most well documented evidence of response to selection in plants comes from plant breeding studies which use some regime of selection other than mass selection. And, of course, comparisons between

closely related taxa of different breeding systems are scarce, so one is forced to deal with experiments on plants with particular breeding systems as a group.

Outcrossed taxa

The best example of long term mass selection in an outcrossed taxon is the 70 generation experiment selecting for oil and protein concentration in Zea mays, summarized by Dudley et al. (1974). The four populations selected for extremes in concentration have continued to show a significant response for 70 generations, with the means of the high protein, low protein, high oil, and low oil strains in generation 70 being respectively 215%, 23%, 341%, and 14% of the means of the original population. Zea mays has also been successfully selected for increased proflicacy (24% in 6 cycles of selection) and grain yield (18% in 6 cycles) (Arboleda-Rivera and Compton, 1974), increased yield (20% in 4 cycles) (Gardner, 1961), increased earworm resistance (28% in 10 cycles) (Zuber et al., 1971), increased cold germination (36% in 4 cycles) (McConnell and Gardner, 1979), and increased and decreased ear length (Cortez-Mendoza and Hallauer, 1979).

Another outcrossed species which has been the subject of successful mass selection experiments is Medicago sativa. Response has been observed to selection for increased resistance to bacterial wilt (38% in 4 cycles) (Barnes et al., 1971), increased self-sterility (77% in 2 cycles) and self-fertility (103% in 2 cycles) (Busbice et al., 1975), (73% in 3 cycles) (Villegas et al., 1971), resistance to anthracnose (67% in 3 cycles) (Devine et al., 1971), and increased (300% in 2-3 cycles) and decreased (66% in 2-5 cycles) saponin levels (Pedersen et al., 1973).

In Ipomoea batatas mass selection has produced response in terms of decreased oxidation of the root flesh (Jones, 1972) and changes in a complex composed of a number of economically valuable characters (Jones et al., 1976). In Agropyron desertorum Schaaf (1968) has successfully selected for extremes of seed size (±7% in one cycle) and increased seed yield. Brassica hirta (Sinapis alba) has been selected for extremes of oil content (+16%, -14% in 8 cycles) (Olsson and Andersson, 1963). Extremes of flowering time were successfully selected in Brassica campestris var. brown sarson by directional selection (+0.3%, -10% in 3 cycles) (Murty et al., 1972). Beta vulgaris has been selected for extremes of dry matter content in the root (+35%, -40% in 13 cycles) (Josefsson, 1963). Limnanthes alba has responded to two cycles of selection for flowering time (+13%, -11%) (Jain, 1979). This is one situation where a closely related inbreeding species (L. floccosa) exists and has been studied for levels of genetic variability, but unfortunately no selection experiments have been done on it yet.

Inbreeding taxa

There are a number of studies of response to mass selection in inbreeding taxa. In Avena sativa, response has been observed to selection for increased panicle weight (15% in 2 cycles) (Chandhanamutta and Frey, 1973), reduced plant height (2 inches in 4 cycles) (Romero and Frey, 1966), and to one cycle of divergent selection for heading date (±22%), plant height (+5%, -4%), grain yield (±9%), width of seed (+5%, -3%), seed weight (+5%, -3%), and number of spikelets per panicle (+5%, -1%) (Geadelmann and Frey, 1975). In Avena fatua successful divergent selection has produced changes in growth habit (+13%, -31%), flowering time (+13%, -28%), and height (+10%, -15%) in

one cycle (Imam and Allard, 1965). As noted earlier, both A. fatua and its more highly selfed relative A. barbata have been selected for increased and decreased seed size and heading date (Jain and Marshall, 1970). Glycine max has been selected for extremes of seed size (+10%, -4% in 3 cycles) and specific gravity of seeds (Fehr and Weber, 1968). Divergent selection for 10 cycles in Sorghum bicolor has changed the mean seed weight (+34%, -18%), plant height (+31%, -26%), and flowering time (+10%, -2%) (Foster et al., 1980). Four cycles of mass selection for increased green weight of leaves in Nicotiana tabacum resulted in an increase of 18% (Matzinger and Wernsman, 1968). Allard et al. (1968) in their review of the genetics of inbreeding species report successful selection for intensity of coat colour in seeds of Phaseolus lunatus, and extremes of seed size in P. lunatus (± 7.5% in 4 cycles), P. vulgaris (±4.5% in 4 cycles) and barley. In Eleusine, Hilu and deWet (1980) were able to increase germination rates by 20-100% in 4 cycles of selection in three species, E. indica, E. coracana, and E. tristachya.

As has been the case with selection experiments in nearly every organism, plant or animal, and for nearly every character studied, enough genetic variability is present in both breeding system groups for a response to selection to occur. One potential problem which should be mentioned is that negative results (in this case, lack of response to artificial selection) may not be reported in the literature. Given the investment in time and effort involved in most careful selection experiments, this is probably not in fact a problem, and it appears from the evidence examined here that both outcrossed and selfed taxa show considerable response to selection for a number of characters. It is only from studies such as that with Avena fatua and A. barbata, which comes close to meeting the ideal conditions of relatively natural levels of genetic variability, natural breeding systems, and

mass selection, that the most useful comparisons may be drawn.

Breeding system, genetic variability, and the response to selection in *Plectritis*

The objective of this study was to examine the responses to divergent artificial selection of two natural populations of plants which differ mainly in their breeding system. If differences in selection response were observed, this could reflect differences in the amount and / or organization of the underlying genetic variability.

The plants chosen for this study were the two species of *Plectritis*, *P. congesta* and *P. brachystemon*. There are a number of features of the two species which make them ideal for this purpose. The two species are very closely related. Morey (1962), in the most recent treatment of the genus, considered them subspecies of *P. congesta*. Hitchcock and others have not even given them that rank, considering them one species (Hitchcock and Cronquist, 1973). The species are very difficult to distinguish before they have flowered, since they have nearly identical vegetative habit. Populations of the two grow sympatrically in a number of locations, and even when allopatric they occupy the same type of habitats, that is, thin, edaphically dry substrates on rocky coastal bluffs and headlands, and open slopes and clearings inland, with the same community of associated annual and perennial herbs. It is safe to assume that the large scale selective pressures that they have encountered in terms of habitat have not differed significantly between the two species for many generations.

Nevertheless, the populations of the two species which occur in British Columbia are quite distinct, differing in a number of floral morphological characters (flower colour and size, degree of protandry, nectar

production) which also reflect their basic breeding system difference. Plectritis congesta is largely outcrossed, with a mean outcrossing rate measured in a number of populations and over a number of seasons of 70%; P. brachystemon is highly selfed, with a mean outcrossing rate of less than 2% (Carey and Ganders, 1980; Ganders et al., 1977a., 1977b.; Layton, 1980). In addition, the two species have proved to be intersterile in laboratory crosses, and no intermediate forms have been observed in a number of locations where the two grow sympatrically. In effect, the only major biological difference between the two species appears to be their breeding system.

Both species are small, relatively easy to grow in crowded conditions in greenhouses or controlled environment chambers, and complete their life cycle, seed to seed, within 5 months under suitable conditions.

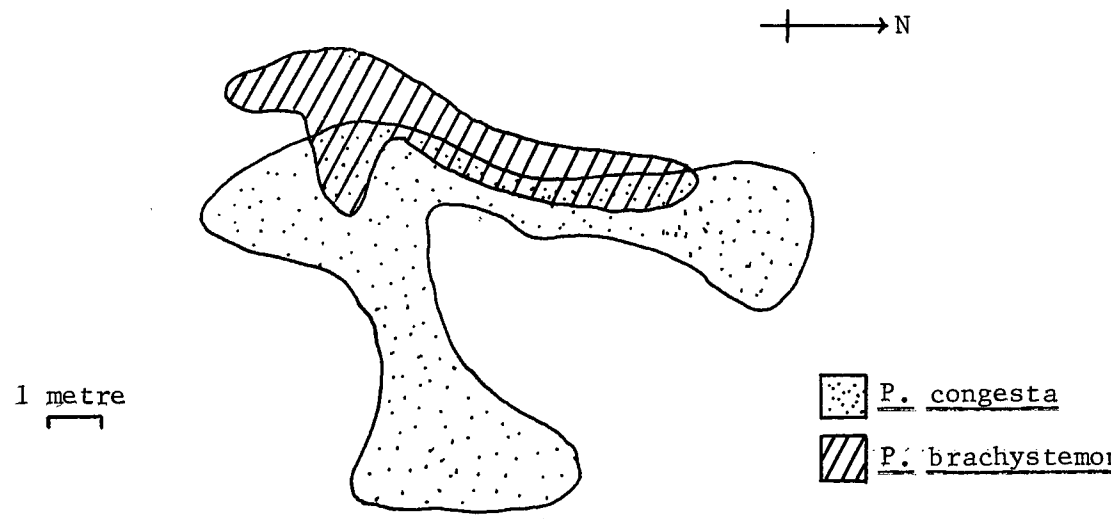
In addition, independent estimates of genetic variability are available for the two species from two studies. Isozyme data has been analysed to determine levels of within and between population diversity in a number of populations of both species (Layton, 1980). Morphometric characters of the fruits have also been examined in populations of each species (Ganders and Maze, unpublished).

Materials and Methods

Source populations

The seed for the base populations of the two species came from two populations (one of each species) growing sympatrically in Mill Hill Park near Victoria on southern Vancouver Island, British Columbia, Canada. Both local populations are part of more extensive populations covering the open hillsides in the park, more or less continuously in the case of *P. congesta*, but in isolated pockets in the case of *P. brachystemon*. The habitat is typical for the species: open, rocky hillsides with patches of shallow soil, wet in winter and edaphically dry by early summer, with a community of grasses, bryophytes, and herbaceous winter annuals and perennials under scattered *Quercus garryana*, *Arbutus*, and *Cytisus*. Nine hundred sixty three plants of *P. congesta* and 590 plants of *P. brachystemon* were collected in late fruit in June 1977. These numbers probably represent 50 - 75% of the total numbers in the local population. The extent of the two local populations collected and their overlap is diagrammed in Figure 1. The numbers of fruits per plant in the populations varied from 1 or 2 to many; all fruits were collected from each plant. I made no effort to collect equal numbers of fruits from each plant, and fruits from each species were lumped in bulk samples. Frequencies of winged and wingless fruited plants were recorded in *P. congesta* for use in a progeny test to determine outcrossing rate. The winged and wingless fruits were bulked separately. All plants of *P. brachystemon* at this locality are wingless fruited.

Figure 1. Source *Plectritis* populations: Mill Hill Pk., June 1977.



Growing conditions

All plants in the experiment were grown in standard 25 x 50 cm plastic flats. Fruits were planted 1 cm deep in approximately 4 cm of steam treated soil. The fruits were planted 200 to a flat in a grid of 10 rows and 20 columns spaced 2.5 cm apart. Fertilizer (Hi-Sol 20-20-20) was added to the soil prior to planting, to remove some possible sources of heterogeneity within and between flats in nutrient levels. The amount of fertilizer added varied from generation to generation, as higher levels in the early generations caused excessive growth, which made the plants difficult to handle (Table I). All experimental populations were grown in a single Conviron walk-in controlled environment chamber. The conditions of light and temperature were set as much as possible to simulate natural conditions; the plants were germinated in a cold chamber, and then light and temperature were increased as the plants matured. The light and temperature conditions varied slightly from generation to generation as I attempted to find the best compromise between a short generation time and a plant habit best suited for manipulation (short, stocky plants with a strong root system) (Table I).

Positions of the flats in the growth chamber were assigned at random and the flats were shuffled several times during each generation to remove position effects. All flats were watered to saturation daily with tap water until fruit set was complete, and the plants were then allowed to die as the soil dried.

Measurements

All plants in each treatment population and every generation were

Table I. Growing conditions

Generation	Fertilizer (gm/flat)	Temperature (C night/ C day)	Light (hr dark/hr light)	Notes
G_0	8	7/12 - 39 days 10/15 - balance	8/16	-growth chamber out of operation day 82 - day 89, plants at room temperature -sprayed for aphids (Isotox) day 103
G_1	8	7/12 - 39 days 10/15 - balance	8/16	
G_2	4	7/12 - 42 days 10/15 - balance	8/16	-sprayed for mildew (Benomyl) day 39
G_3	4	7/12 - 33 days 10/15 - 38 days 12/20 - 64 days 12/23 - balance	8/16	
G_4	2	7/12 - 28 days 10/15 - 12 days 10/18 - 18 days 11/20 - balance	8/16	-intensity of light during day increased day 79
G_5	2	7/12 - 28 days 10/15 - 8 days 11/20 - balance	8/16	

measured for the following characters:

1. Days to emergence

The number of days between planting and the complete emergence of the cotyledons above the soil surface was recorded.

2. Days to anthesis (flowering time)

The number of days between planting and the opening of the first flower on each plant was recorded.

3. Height at anthesis

The height of the plant in mm, from the soil surface to the top of the main inflorescence (Figure 2) was recorded on the first day of anthesis.

4. Number of nodes at anthesis

The number of nodes between the soil surface and the base of the main inflorescence (inclusive) was recorded for each plant on the first day of anthesis. In P. brachystemon, in which the upper nodes are still highly compressed at anthesis, the nodes were counted by identifying pairs of leaves at each node.

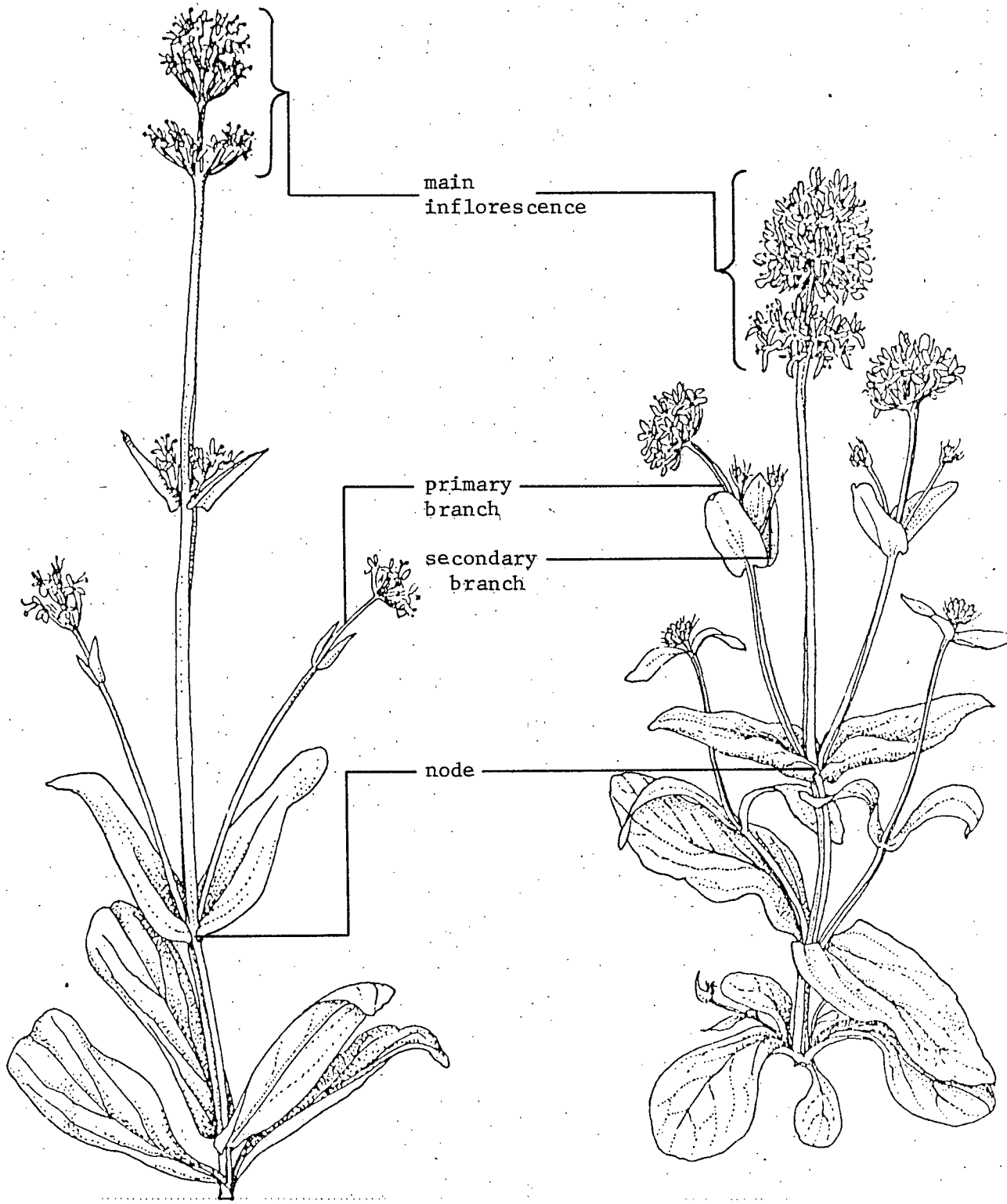
5. Number of primary branches at anthesis

The number of branches or branch buds visible in the axils of leaves on the main axis on the first day of anthesis was recorded. This is an underestimate of the total amount of branching, as there are some primary branches, as well as secondary, tertiary, and higher order branches, which do not begin to develop until later in the flowering period (Figure 2).

6. Fruit production

The ripe fruits were collected from the main inflorescence of each plant and counted. This figure is subject to a large amount of experimental error; fruits, when ripe, are easily dislodged from the plant and lost, and P. congesta requires artificial pollination to produce fruit well in the laboratory, so unavoidable variation in pollination levels will have

Figure 2. Morphology of Plectritis.



Plectritis brachystemon x .55

Plectritis congesta x .45

affected fruit set in this species.

7. Fruit phenotypic characters

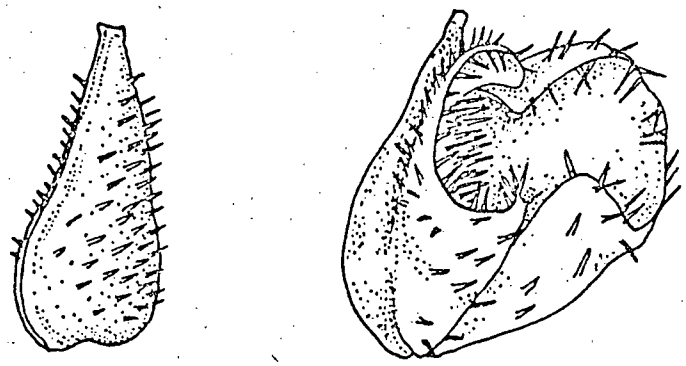
The fruit from each plant was scored for a number of phenotypic characters. Fruits of P. brachystemon were all monomorphic (in this case) for these characters. In P. congesta, fruits could be scored for wing phenotype (winged or wingless, see Figure 3), pubescence pattern (Figure 4), fruit colour (body and wings scored separately on the basis of an arbitrary colour classification using 4 colour classes), and the presence in winged fruits of a characteristic indentation in the margin of the fruit wing. I attempted to record the shape of the fruit wing, which varied considerably between plants and relatively little within plants. The variation, however, was too continuous and complex to allow for an adequate scoring system and not amenable to any simple measurement.

In addition to these characters, I recorded various other sporadic and anomalous characters including: aberrations in the number of cotyledons, presence of more or less fused cotyledons, chlorotic seedlings, excessively darkly pigmented seedlings, abnormal branching patterns and other abnormalities in the adult growth habit, and abnormalities in flowering characteristics, most commonly aborted anthers and lack of good pollen, as well as flowers with abnormal numbers of parts (for example, more than 5 corolla lobes, more than three stamens, etc.).

Breeding procedure

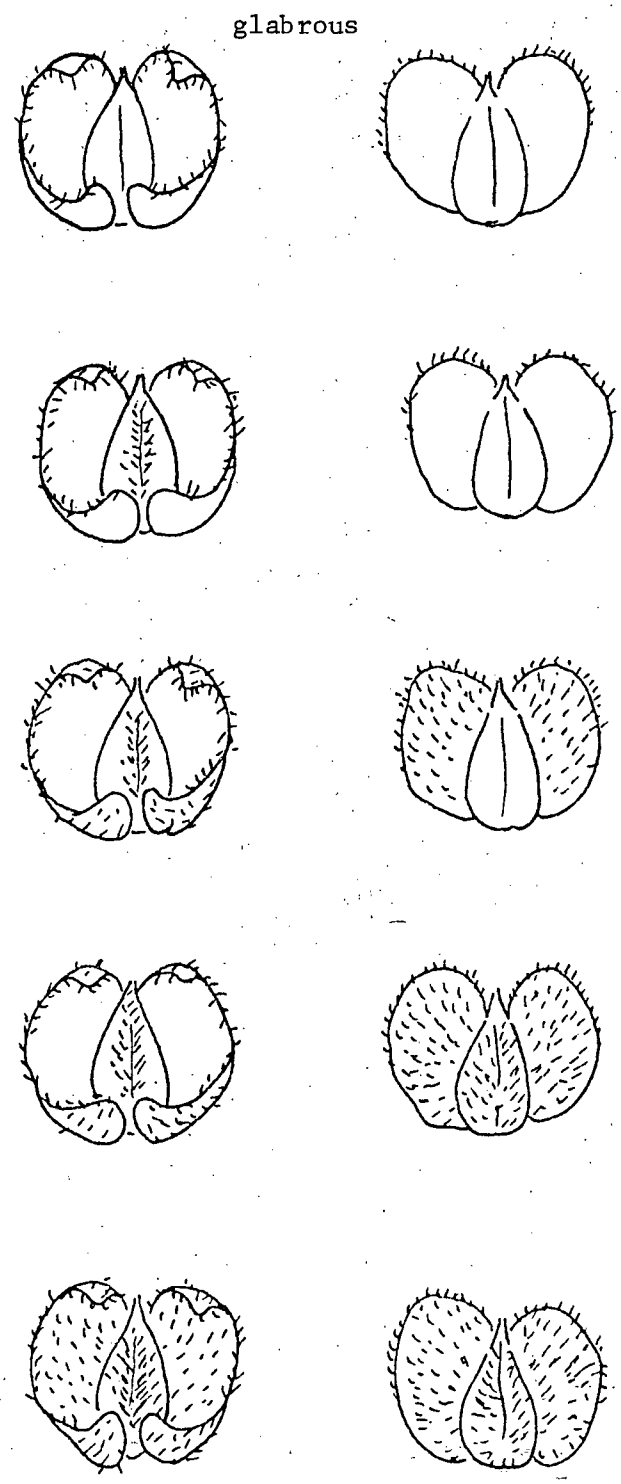
Three groups of populations were involved in the experiment, based on a combination of species and breeding procedure. Plectritis congesta required manual pollination because it is protandrous and does not

Figure 3. Plectritis fruit wing phenotypes.



Wingless Winged

Figure 4. Fruit pubescence phenotypes in winged Plectritis congesta fruits



automatically self-pollinate successfully in the growth chamber. I took advantage of this to set up two groups of P. congesta populations, one outcrossed and one selfed. The plants in each population were either self-pollinated or crossed to relatively unrelated plants (not siblings). The pollination was done by removing newly opened anthers with fine forceps from the pollen parent, and using them to pollinate appropriate stigmas. The success of this breeding procedure was evaluated by examining particular progenies in subsequent generations. Plectritis brachystemon is not protandrous, self-pollinates automatically, and sets fruit very successfully in the growth chamber; it is not easy to outcross, because of the small size of the flowers. For these reasons only selfed populations of P. brachystemon were involved in the experiment.

Selection procedure

The selection method was simple individual or mass selection, in which certain individuals of one generation were selected on the basis of their phenotype to produce seed for the next generation. The selection pressure was approximately 90%, that is 20 plants were selected from the 200 in a particular population to form the next generation. Lines were selected separately for short height at anthesis, tall height at anthesis, early anthesis, and late anthesis. An unselected control line was also maintained for each species group. One flat was planted with the last generation, containing 100 individuals of each species from the source populations; this served as an external control to changes which might have affected the internal, unselected control lines. These populations are designated P. congesta G_5 source and P. brachystemon G_5 source.

Base population

The first generation, base populations (G_0) consisted of 9 populations of 200 individuals, 3 each for the 3 species groups: P. congesta outcrossed (PCO); P. congesta selfed (PCS), and P. brachystemon selfed (PBS). For each group there was a control population, an anthesis population, and a height population. The fruits from which the base populations were grown were selected at random from the bulk sample from the source populations. Winged and wingless fruits in the PCO and PCS populations were planted in frequencies equal to their frequencies in the source population (12.5% wingless, 87.5% winged).

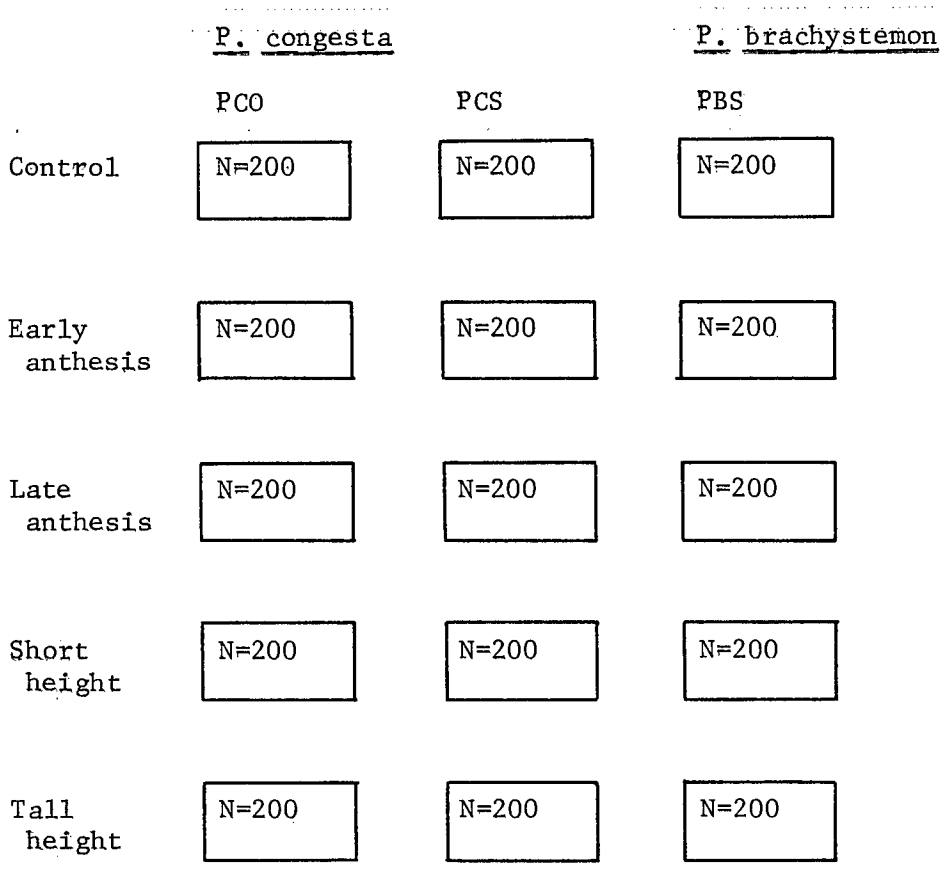
First cycle of selection

From the base populations, 20 plants were selected as parents for the next generation, G_1. Ten fruits from each were taken to form a population of 200. Selection lines for early and late anthesis were begun by taking the 20 earliest and latest flowering plants in the G_0 anthesis population as parents. Similarly, short and tall lines were selected from the G_0 height population. Twenty plants were selected at random from the G_0 control population to form the G_1 control population. Thus there were 15 treatment populations in G_1 and subsequent generations as indicated in Figure 5.

Subsequent cycles of selection

In each generation from G_1 on, the 20 earliest, latest, shortest, and tallest plants were selected in the respective populations as parents for

Figure 5. Experimental populations maintained through 5 generations of selection, G_1 to G_5.



the subsequent generation. Again, the control lines were continued by selecting plants at random from the control populations. In all selections in PCO the pollinations were made, as far as possible, between selected individuals of different families. The requirement that 10 fruits be produced before a plant qualified as a parent for selection meant that some individuals which would otherwise have been selected on the basis of their flowering time or height were disqualified. In effect, there was selection for a minimum level of fecundity in addition to selection for height and flowering time. In G_3 the PCS and PBS populations selected for short height produced too few fruits per individual to even reach the minimum fecundity level, so I had to reduce the family size of 10 in this case. Thirty-seven individuals from PCS short and 35 from PBS short were selected to contribute families of varying size (1 - 10 progeny) to the next generation G_4.

Progeny test and outcrossing rate in P. congesta

The winged and wingless phenotype frequencies in the source population, together with the observed frequencies of winged and wingless morphs in their progenies (G_0) allowed a progeny test which gave an estimate of the outcrossing rate, t, in the source population (Ganders et al., 1977a.).

Data treatment and analyses

All measured or scored characters in every line and generation were punched on computer cards and stored in files in the University of British Columbia computer system for analysis. Most statistical analyses were performed using the MIDAS statistical package (Fox and Guire, 1976).

Metrical characters

I used the six metrical characters - days to emergence, days to anthesis, height at anthesis, number of nodes at anthesis, number of primary branches at anthesis, and fruit production - to compute a further set of six transformed characters as follows. The grand mean and standard deviation of each were computed for all six *P. congesta* G_0 populations together, and for all three *P. brachystemon* G_0 populations together. In data for subsequent generations, all populations within a particular species group were transformed by a multiplicative and an additive factor, so that the distribution of the transformed character in the control (unselected) population had the same mean and standard deviation as the G_0 standard. An example is given in Figure 6. This transformation effectively removes the following two sources of variation from the data, which would otherwise interfere with the interpretation of the experimental results: 1. the common effects of generation to generation fluctuations in growing conditions and other environmental factors, and 2. the effects of any uncontrolled selection pressures (for example, selection for growth under growth chamber conditions) and to some extent the effects of inbreeding which could be presumed to be acting equally on selected and unselected lines.

Descriptive statistics

The distributions of the metrical characters, raw and transformed, were described in all populations in terms of number of individuals measured, maximum and minimum values observed, population mean, standard

Figure 6. An example of data transformation procedure used on metrical characters.

Days to emergence

	G_1 raw data			G_1 transformed			G_0 standard	
	$\bar{x}$	s.d.	correction	$\bar{x}'$	s.d.'	=	$\bar{x}$	s.d.
PCO control	20.77	5.55	$X_i \times 0.7522 + 2.776 = X_i'$	18.4	4.17	=	18.4	4.17
PCO early	21.03	4.47		18.6	3.36			
PCO late	21.81	5.17		19.2	3.89			
PCO short	19.43	4.08		17.4	3.07			
PCO tall	21.22	5.53		18.7	4.16			

deviation, coefficient of variation, skewness, and kurtosis. In addition, frequency histograms of all distributions were generated to depict them graphically.

Comparisons between distributions

For every metrical character the distributions of the selected populations were compared to those of the control in the same generation (for example, PCO early G_2 vs. PCO control G_2) by means of Kruskall-Wallis tests (non-parametric analysis of variance). The transformed data were also compared between generations within lines by means of Kruskall-Wallis tests (for example, PCS short G_4 vs. PCS short G_5).

Correlations

Correlations between all pairs of metrical characters within each population were calculated by Spearman's rank correlation procedure.

Heritability estimates

Estimates of narrow sense heritability (h^2, the proportion of the total phenotypic variance in a population which is attributable to additive genetic effects) were calculated in the experimental populations for the selected characters, flowering time and height at anthesis, by two methods. Realized heritability was calculated after the method of Hill (1972). This estimate is based on the ratios of selection differential (selection pressure) to response in lines under divergent selection. Heritabilities

were also calculated for all metrical characters by the method of parent-offspring regressions in the control lines (Falconer, 1960).

Variance within populations

The components of variance within populations were analyzed by univariate ANOVA for the metrical characters. The variance was partitioned into components between families and within families.

Other characters

Frequencies of fruit wing phenotypes, pubescence patterns, fruit wing and body colours, presence of wing indentation, and aberrant characters were tabulated for every population.

Results

Breeding systems in Plectritis congesta and P. brachystemon

Outcrossing rates in the source populations (Mill Hill Pk., 1977)

The outcrossing rate in the P. congesta source population in 1977 was estimated by the progeny test method (Ganders et al., 1977a) to be 61.6%. This is based on a total sample of 1175 individuals grown from seed. This estimate compares well with other estimates of outcrossing rates in populations of the species, which have averaged around 70% (Ganders et al., 1977a; Carey and Ganders, 1980; Layton, 1980).

Since the source population of P. brachystemon was monomorphic for all of the morphological markers which might have been used in a progeny test, no estimate of the outcrossing rate is yet available for it. There is no reason to expect this population to differ substantially from others measured throughout the range of the species in British Columbia. Ganders et al. (1977b) and Layton (1980), using the fruit wing polymorphism and allozyme polymorphisms respectively, estimate that the average outcrossing rate in P. brachystemon is 2%, and no populations were found exceeding 5%.

Outcrossing rates in the experimental populations

The effect of the experimental breeding system as practised can be roughly estimated in P. congesta by examining particular progenies as follows. In the selfed group, PCS, the progenies of wingless fruited plants (homozygous recessives) can be scored to obtain the frequency of winged

fruited progeny, which are necessarily the result of outcrossing events. This frequency will underestimate the actual rate of outcrossing, as a (small) proportion of the wingless fruited progeny are likely also to be the result of outcrosses to other homozygous recessive or heterozygous plants. In the outcrossed group, PCO, progenies of wingless fruited plants which have been crossed to homozygous dominant winged fruited plants can be scored to obtain the frequency, x, of wingless fruited offspring. If these were all the result of accidental selfing, the outcrossing rate would be 1 - x. In practice this estimate is again an underestimate of the actual outcrossing rate, as some of the wingless fruited progeny are again likely to be the result of accidental outcrosses, in this case to some plant other than the pollen parent of record. The error in these estimates is likely to be large, and mostly depends on the allele frequencies in the populations (the higher the frequency of the recessive allele, the larger will be the error); nevertheless, the estimates are of interest, and are given in Table II.

Characteristics of the base populations

Descriptive statistics of the metrical (quantitative) characters

The initial distributions of the various measured characters in the base populations, G_0, of the two species are given in Table III. Under the experimental conditions in the growth chamber, P. brachystemon emerges later, grows taller, produces more nodes and more primary branches, flowers later, and produces more fruit than P. congesta. Examining the coefficients of variation, which are scale free estimates of the phenotypic variability,

Table II. Estimates of outcrossing rates in the experimental populations.

P. congesta selfed

Population		Number of progenies	Estimated outcrossing rate
PCS control	G_0	3	0.25
PCS late	G_0	3	0.19
PCS short	G_0	5	0.35
PCS tall	G_0	3	0.08
PCS control	G_1	4	0.18
PCS early	G_1	1	0.00
PCS late	G_1	6	0.10
PCS short	G_1	5	0.12
PCS tall	G_1	4	0.04
PCS control	G_2	4	0.05
PCS late	G_2	6	0.22
PCS short	G_2	6	0.06
PCS tall	G_2	6	0.04
PCS control	G_3	4	0.28
PCS late	G_3	7	0.22
PCS short	G_3	17	0.15
PCS tall	G_3	8	0.14
		mean	0.15

P. congesta outcrossed

PCO early	G_0	1	0.80
PCO late	G_0	1	0.60
PCO late	G_1	3	0.59
PCO early	G_2	2	0.68
PCO late	G_2	1	0.29
PCO short	G_2	2	0.94
PCO late	G_3	1	0.67
PCO tall	G_3	1	0.63
		mean	0.65

Table III. Measured characters, base populations.

	N	Mean	Standard deviation	Coefficient of variation
P. congesta				
Days to emergence (number)	905	18.40	4.177	22.70 **[a]
Height at anthesis (mm)	855	223.87	45.121	20.15 **
Nodes at anthesis (number)	855	8.91	1.108	12.43 **
Primary branches (number)	855	2.71	3.417	126.09 **
Days to anthesis (number)	855	95.02	7.379	7.76 *
Fruit production (number)	861	25.10	18.820	74.99
P. brachystemon				
Days to emergence (number)	304	21.08	5.729	27.17
Height at anthesis (mm)	293	302.91	72.618	23.97
Nodes at anthesis (number)	293	11.80	1.656	14.03
Primary branches (number)	293	6.43	6.841	106.40
Days to anthesis (number)	292	116.76	8.088	6.93
Fruit production	291	61.26	28.48	68.80

[a] Asterisks indicate coefficients of variation significantly different from those in *P. brachystemon*; ** at the 1% level, * at the 5% level, according to modified F - tests (Lewontin, 1966).

it appears that P. brachystemon is more variable than P. congesta for days to emergence, height, and number of nodes at anthesis, and less variable for number of primary branches at anthesis and flowering time. There was no significant difference in the coefficient of variation for fruit production.

Frequencies of qualitative characters

Plectritis brachystemon is monomorphic for all the fruit characters scored; the scores for the base populations of P. congesta for pubescence pattern are presented in Figures 7 to 10, and will be discussed later. The phenotype frequencies of winged and wingless fruits planted in G_0 were the same as in the source population (12.5% wingless, 87.5% winged); the phenotype frequencies of the adult plants in G_0 are presented in Figure 11.

Response to selection of the selected characters

Height at anthesis

Means

The mean heights of plants in the populations selected for height at anthesis departed significantly from the control (unselected) population in most generations, the exceptions being PCO short G_1, PCO tall G_1 and G_3, PCS short G_1, PCS tall G_2, and PBS short G_2 (Figure 12). In the case of the P. congesta populations, the means in the selected lines diverged over the course of the experiment with, in most cases, the tall lines being

Figure 7. Frequency of various pubescence types (see Figure 4) in the experimental populations.

a. Pubescence type 0 in PCO populations

b. Pubescence type 1 in PCO populations

c. Pubescence type 2 in PCO populations

Figure 7.

a. PCO type 0

b. PCO type 1

c. PCO type 2

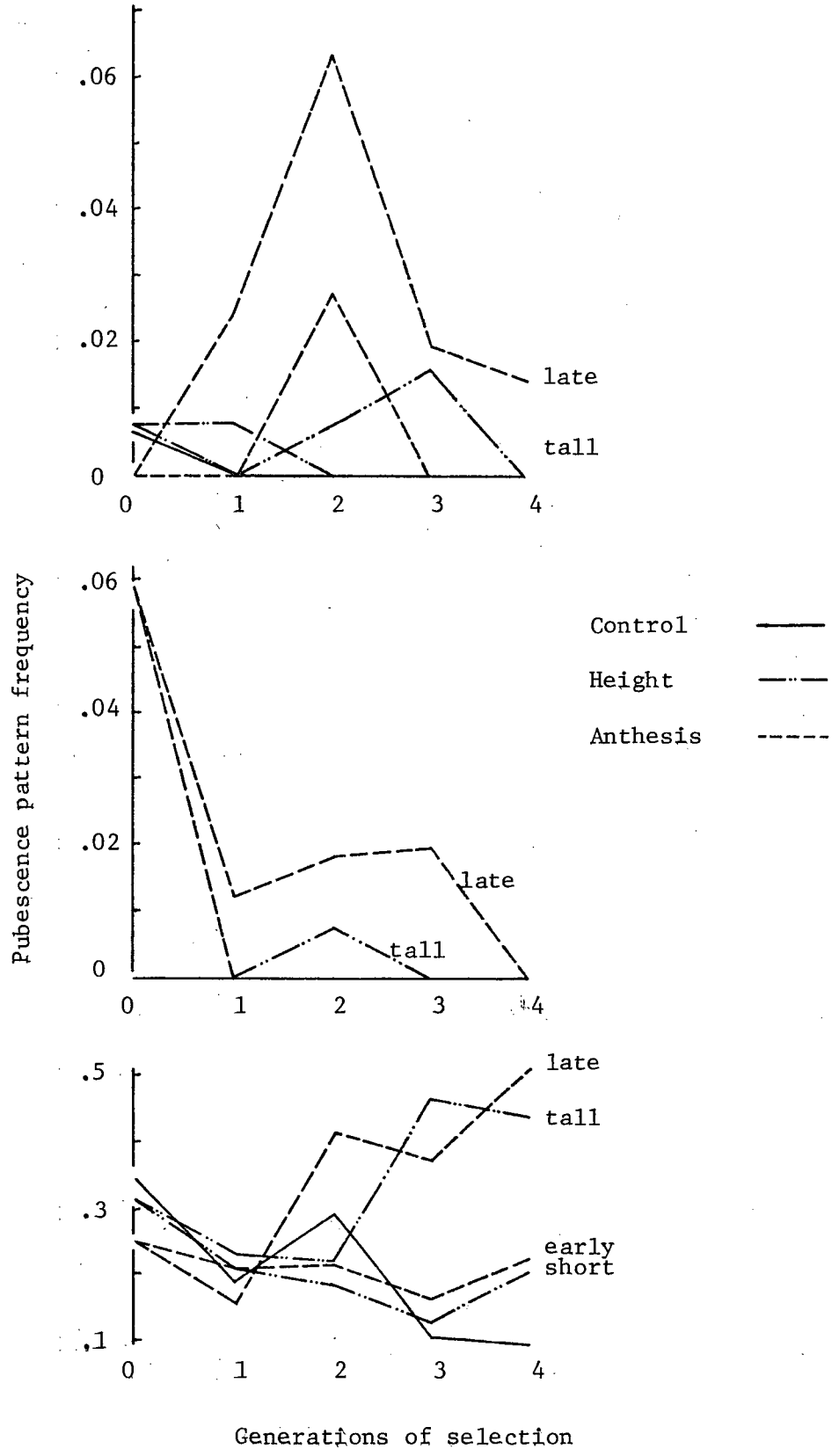


Figure 8. Frequency of various pubescence types (see Figure 4) in the experimental populations.

a. Pubescence type 3 in PCO populations

b. Pubescence type 4 in PCO populations

c. Pubescence type 5 in PCO populations

Figure 8.

a. PCO type 3

b. PCO type 4

c. PCO type 5

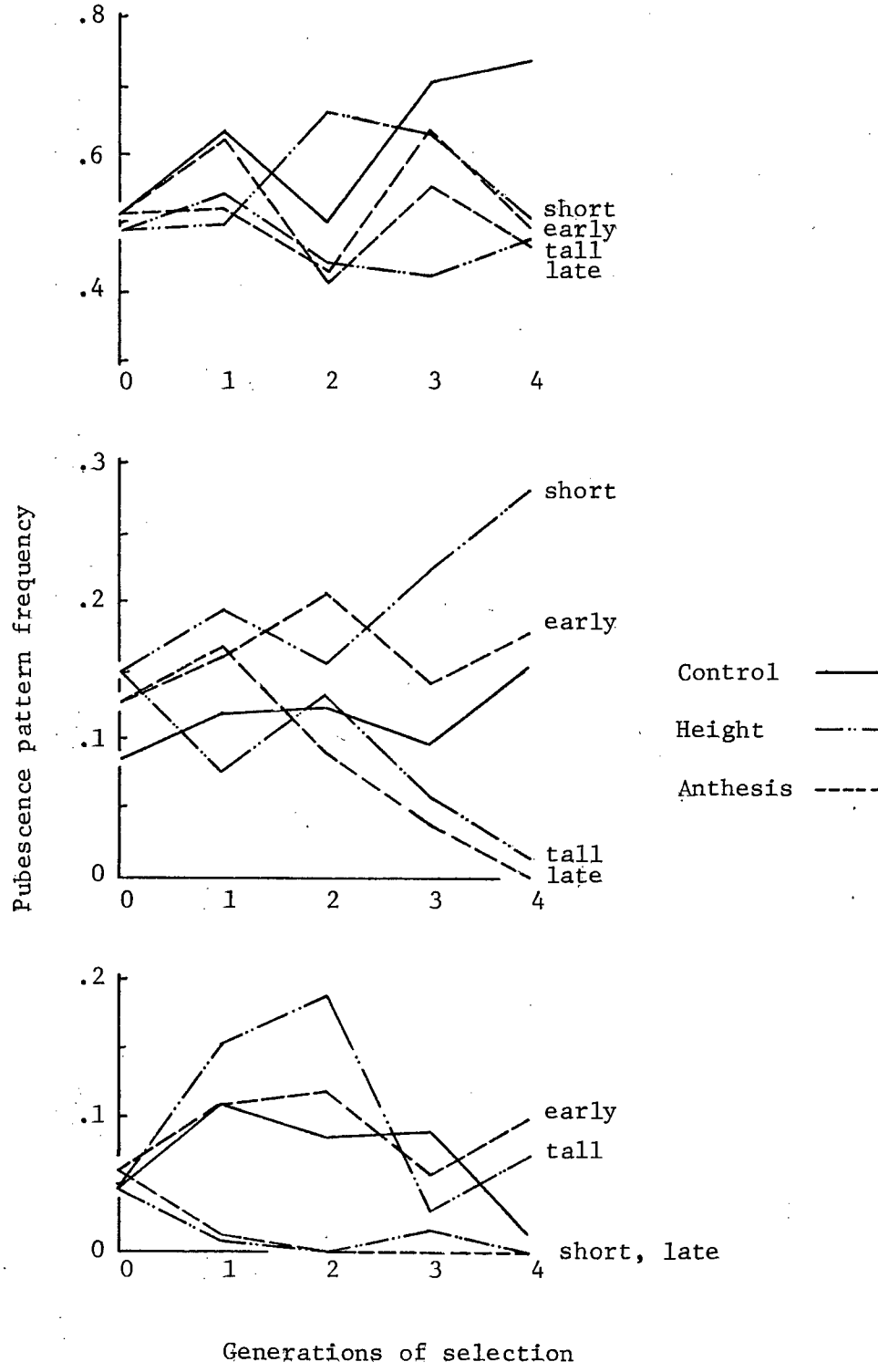


Figure 9. Frequency of various pubescence types (see Figure 4) in the experimental populations.

a. Pubescence type 0 in PCS populations

b. Pubescence type 1 in PCS populations

c. Pubescence type 2 in PCS populations

Figure 9.

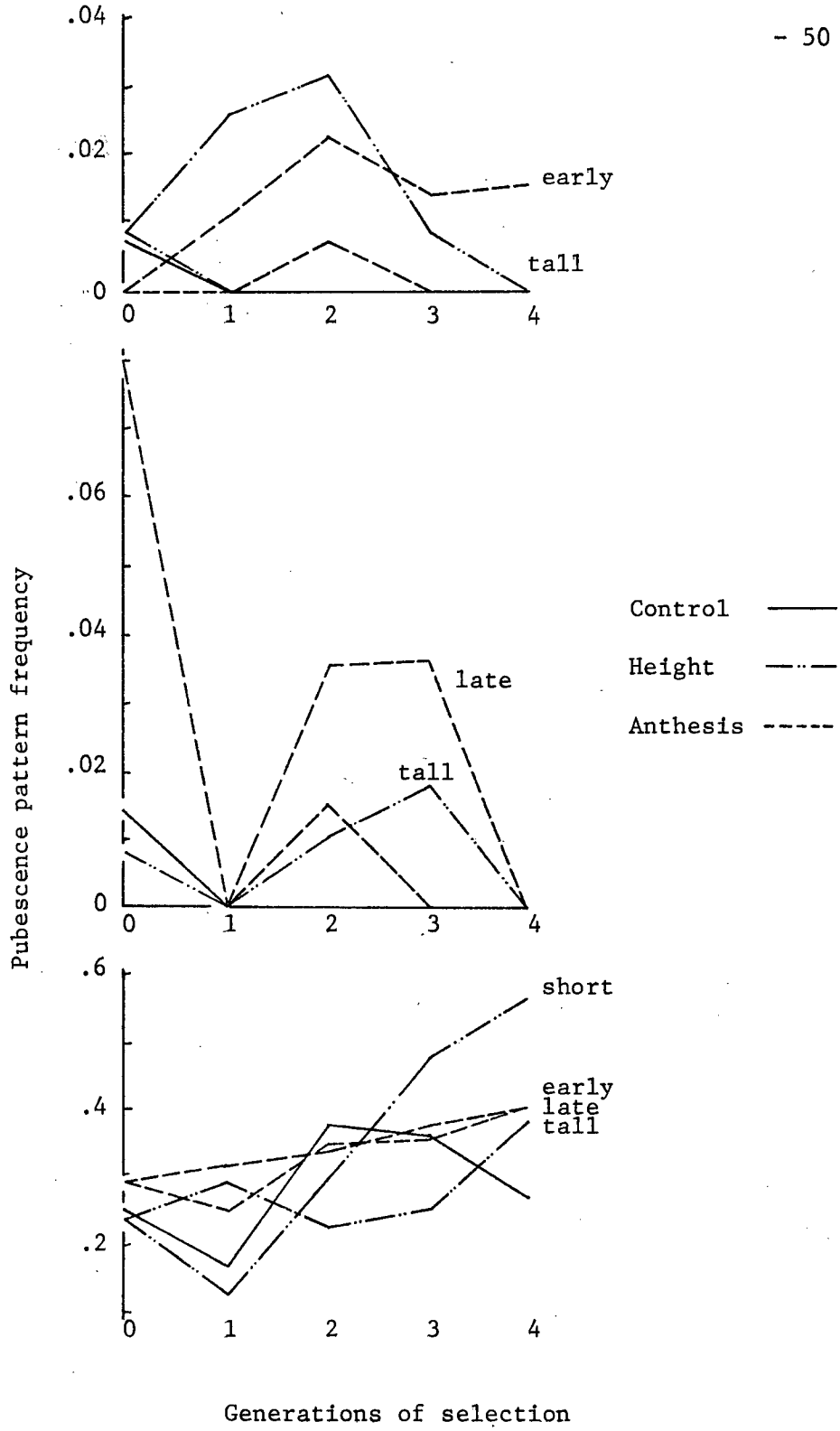

a. PCS type 0
.04
.02
0
early
tall
0
1
2
3
4
b. PCS type 1
.06
.04
.02
0
late
tall
Pubescence pattern frequency
Control
Height
Anthesis
c. PCS type 2
.6
.4
.2
short
early
late
tall
Generations of selection

Figure 10. Frequency of various pubescence types (see Figure 4) in the experimental populations.

a. Pubescence type 3 in PCS populations

b. Pubescence type 4 in PCS populations

c. Pubescence type 5 in PCS populations

Figure 10.

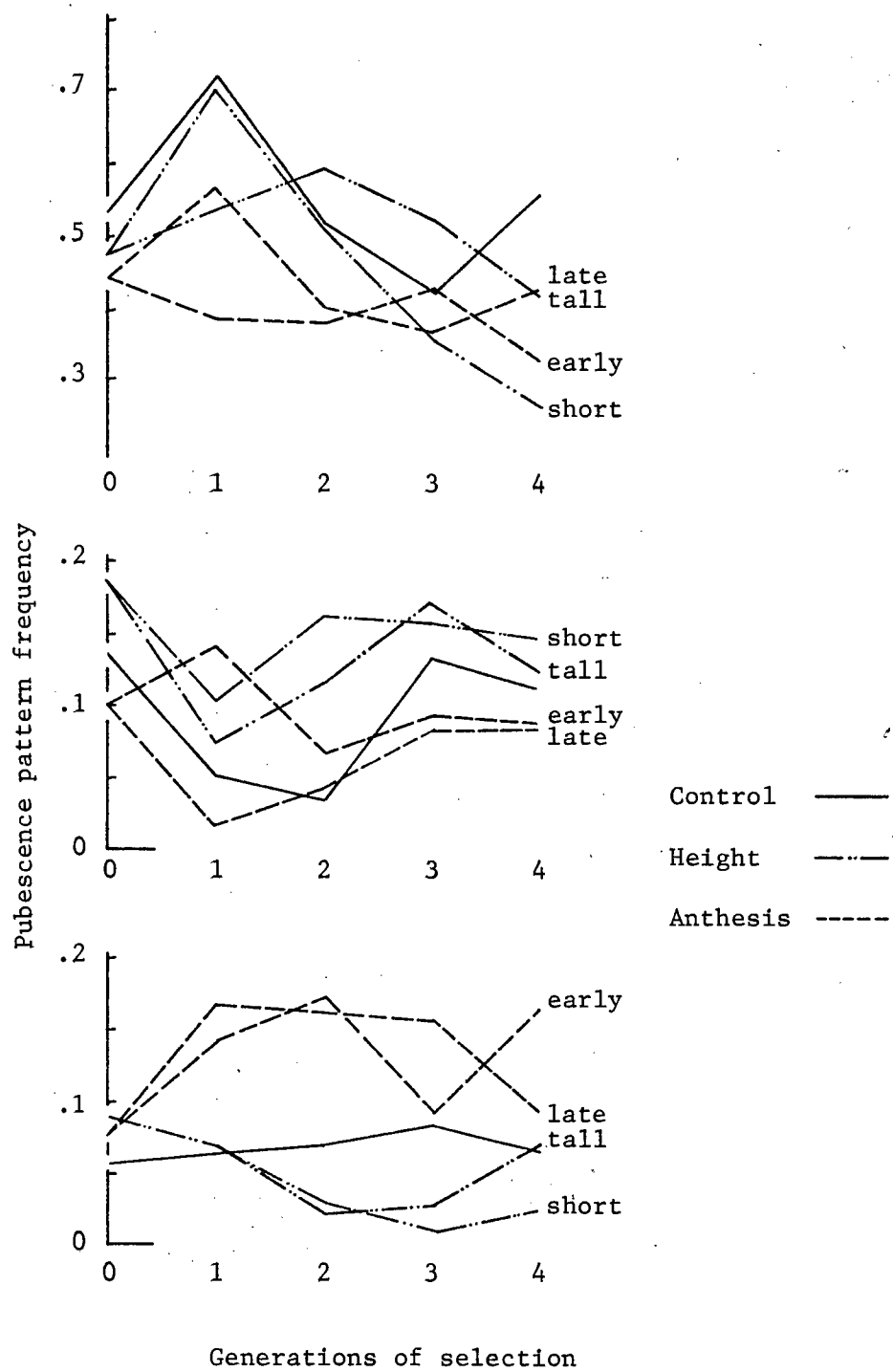

a. PCS type 3
b. PCS type 4
c. PCS type 5
Pubescence pattern frequency
.7
.5
.3
.2
.1
0
0
1
2
3
4
late
tall
early
short
short
tall
early
late
early
late
tall
short
Control
Height
Anthesis
Generations of selection

Figure 11. Frequency of wingless fruited plants in the experimental populations.

a. PCO populations

b. PCS populations

Figure 11.

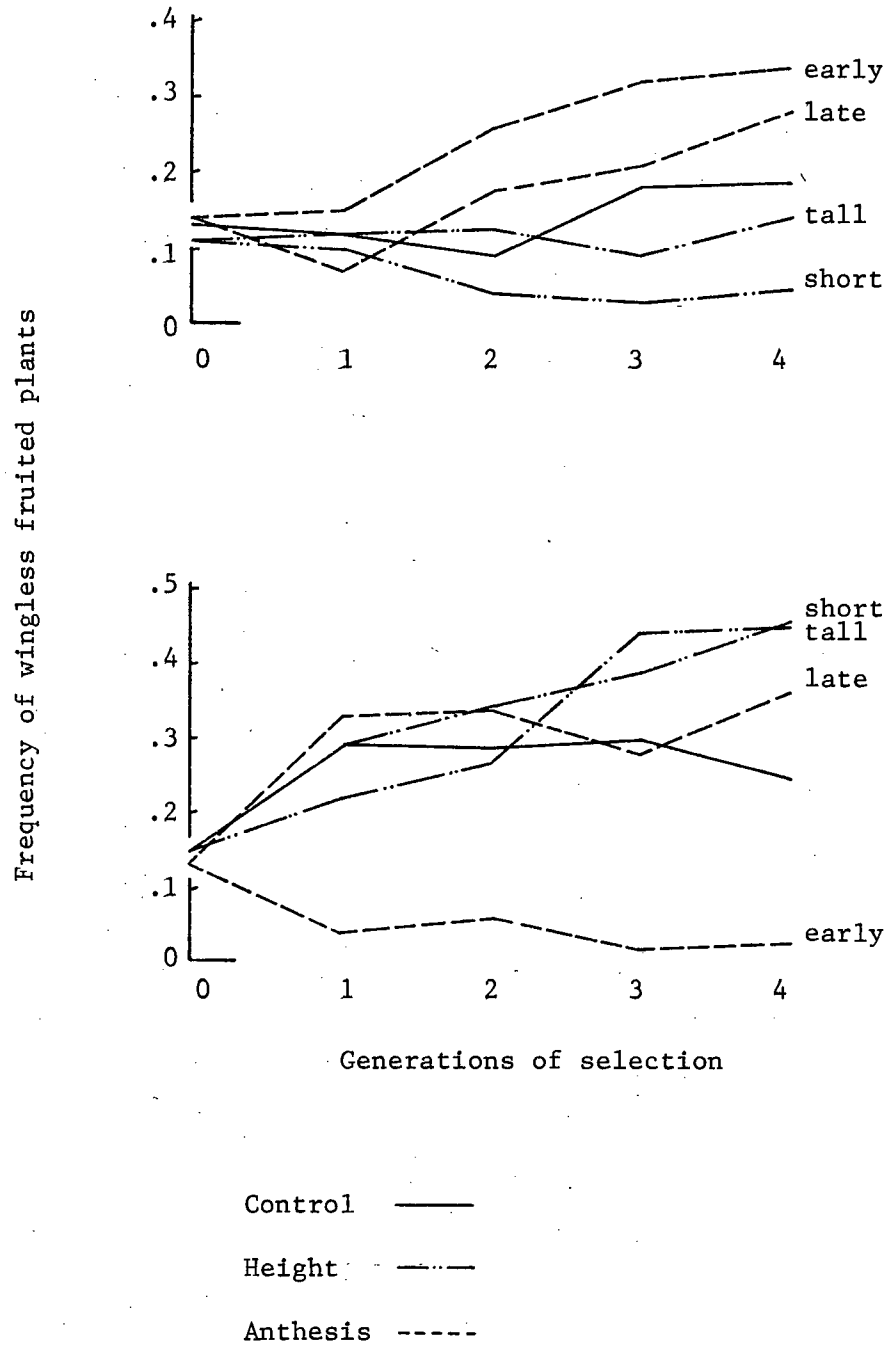

a. PCO
b. PCS
Frequency of wingless fruited plants
.4
.3
.2
.1
0
0
1
2
3
4
early
late
tall
short
.5
short
tall
late
early
Generations of selection
Control
Height
Anthesis

Figure 12. Mean height at anthesis in populations selected for height at anthesis. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

The following pairs of consecutive populations within lines did not differ significantly:

PCO short G_0 and G_1; G_3 and G_4

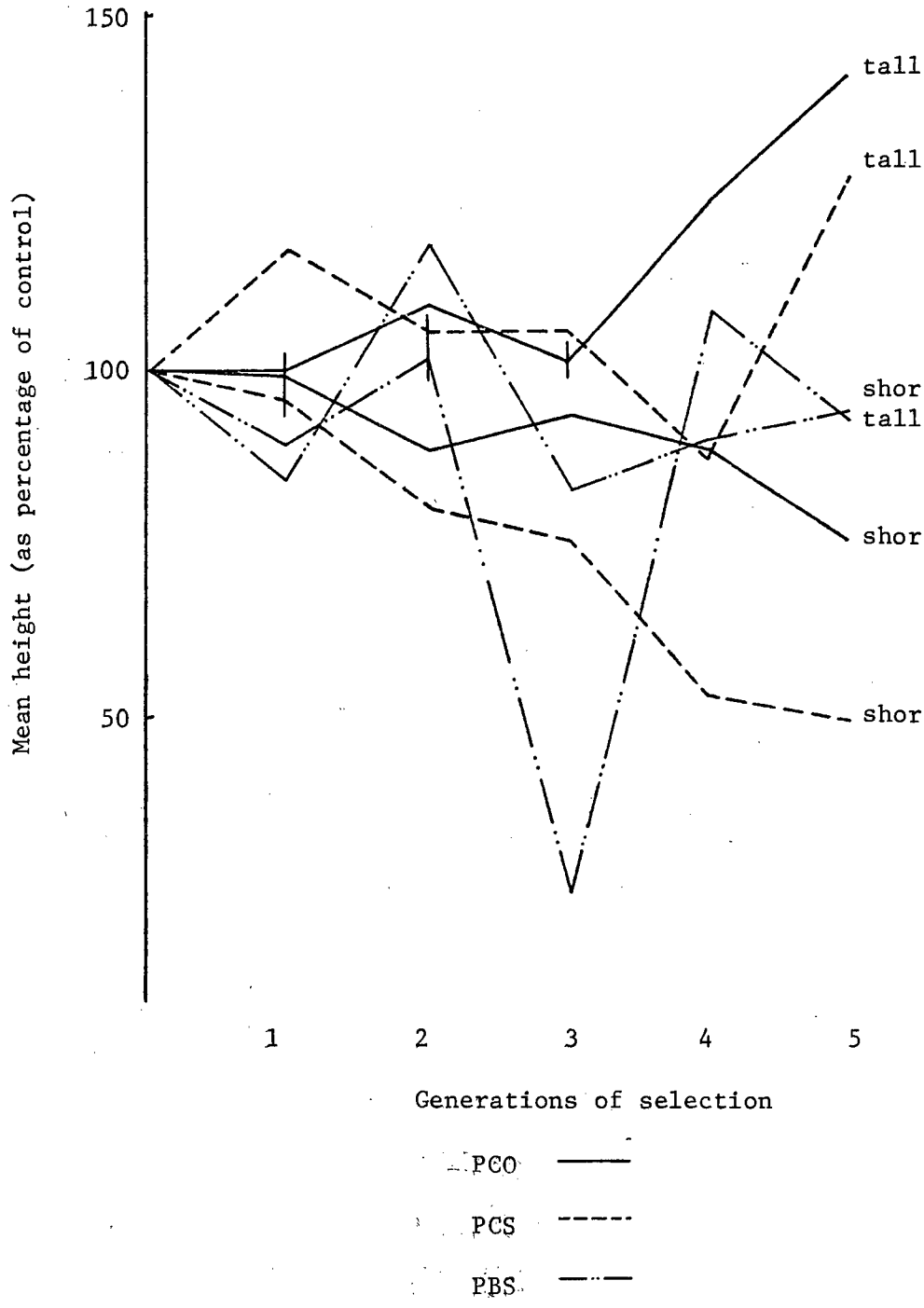
PCO tall G_0 and G_1

PCS tall G_2 and G_3

PCS short G_4 and G_5

PBS tall G_4 and G_5

Figure 12.


150
100
50
Mean height (as percentage of control)
tall
tall
short
tall
short
short
1
2
3
4
5
Generations of selection
PCO
PCS
PBS

taller than the control and the short lines shorter that the control. In PC0 the divergence by the fifth cycle of selection amounted to 66% of the control height (+41%, -25%) or 148 mm (+92 mm, -56mm). In PCS, the divergence by G_5 amounted to 78% of the control height (+27%, -51%) or 175 mm (+61 mm, -114 mm). The means in the P. brachystemon selected lines departed significantly from the control lines, but did not diverge, rather fluctuating erratically with both lines being shorter than the control in G_1, G_3, and G_5, and taller than the control in G_2. In addition, the tall line was shorter than the short line in G_1 and G_4.

The mean heights in the various selected lines were also compared generation to generation and proved to be significantly different in most cases, the following being the exceptions: PC0 short G_1 vs. G_0, G_4 vs. G_3, PC0 tall G_1 vs. G_0, PCS short G_5 vs. G_4, PCS tall G_3 vs. G_2, and PBS tall G_5 vs. G_4.

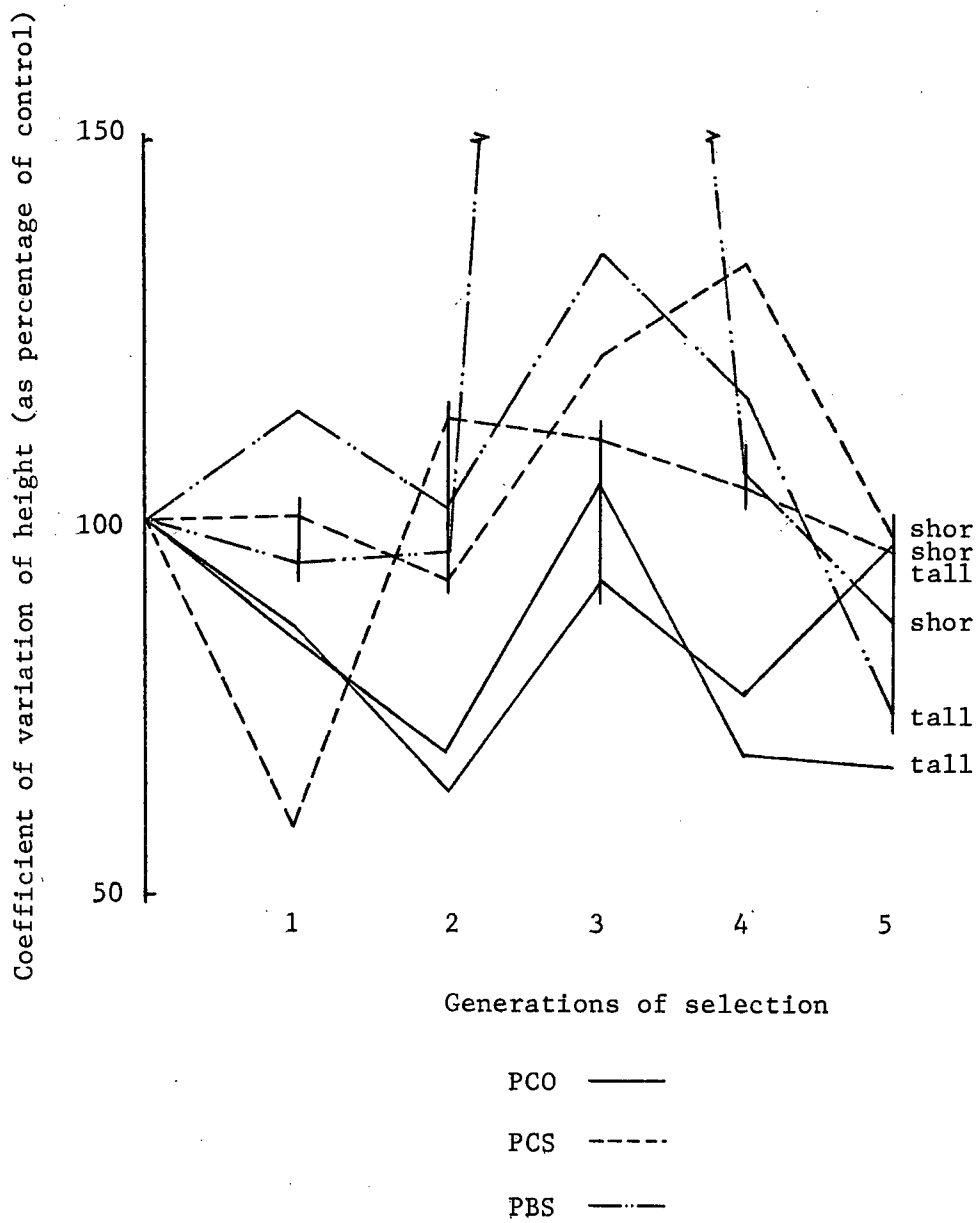
Estimates of variability

Variances

The variances for both the raw and transformed values of height were compared among all populations. The variances in this case are phenotypic, although some of the environmental component has hopefully been eliminated within generations by the use of a common environment, and between generations by correcting the selected population values against an unselected control. Since the variance of a character is dependent on the mean (in a population with a larger mean, the variance will also tend to be larger), the selected lines were compared by means of the coefficients of variation (that is, the standard deviation of the mean as a percentage of the mean) in a modified F - test (Lewontin, 1966) (Figure 13). The

Figure 13. Coefficients of variation for height at anthesis in populations selected for height at anthesis. Coefficients of variation are expressed as a percentage of the coefficients in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

Figure 13.


Coefficient of variation of height (as percentage of control)
150
100
50
1
2
3
4
5
Generations of selection
short
short
tall
short
tall
tall
PCO
PCS
PBS

coefficients of variation in the selected populations were significantly different from the control in 14 out of 30 cases, namely PCO short G_1, G_2, and G_4, PCO tall G_1, G_2, G_4, and G_5, PCS short G_3 and G_4, PCS tall G_1, PBS short G_3, and PBS tall G_1, G_3, and G_4. Of these, six populations showed an increase in variation (PCS and PBS lines) and eight showed a decrease in variation (PCO lines, PCS tall).

Heritabilities

The narrow sense heritability for height at anthesis was estimated two ways. Narrow sense heritability (h^2) is the portion of the total phenotypic variability in a population which can be attributed to additive genetic effects (that is, genetic effects excluding dominance, epistasis, and other interactive effects). Realised heritabilities were calculated after the method of Hill (1972) (Table IV). In the P. congesta lines the heritability of height is significant and approximately equal between the PCS (b_c or h^2 = 0.58) and PCO (b_c = 0.53) lines. Plectritis brachystemon has essentially no heritability for height under the conditions of this experiment. The estimates for PBS in Table IV are bracketed because the method is not meant to be applied in cases where the selected lines diverge in the direction opposite to the direction of selection, as is the case here (see Figure 12, PBS lines in G_1 and G_4). The estimated standard deviations for the heritability estimates are quite large.

The estimated heritabilities from parent-offspring regressions (Table V) are in reasonable agreement with the realised heritability estimates. The P. congesta lines have a fairly large h^2, and there is little difference between the PCS (h^2 = 0.44) and PCO (h^2 = 0.45) lines. Plectritis

Table IV. Realised heritability, calculated using the method of Hill (1972).

		P. congesta		P. brachystemon
		PCO	PCS	PBS
Selection for early or late anthesis	b_c	0.77	0.75	0.49
	$\widehat{sd}_{b_c}$	0.12	0.14	0.22
Selection for short or tall height	b_c	0.53	0.58	(0.06)
	$\widehat{sd}_{b_c}$	0.61	0.64	(0.34)

Table V. Heritability, from parent-offspring regressions*.

		P. congesta		P. brachystemon
		PCO	PCS	PBS
Days to anthesis	h^2	0.60	0.72	0.42
	r^2	0.53	0.55	0.48
Height at anthesis	h^2	0.45	0.44	-0.06
	r^2	0.36	0.30	0.23

* Means of four generations of control populations.

brachystemon again has essentially a heritability of zero for this character. The r^2 values listed estimate the proportion of the total variance explained by the regression, or in other words the goodness of fit of the regression line to the parent-offspring points. The r^2 values for height are fairly low, and quite a bit lower than those for flowering time.

Components of variance

An analysis of variance was performed for all populations between G_1 and G_5, partitioning the observed (phenotypic) variance into components within and between families in each population. It is only in particular cases, such as in progenies in pure breeding lines or in the F_1 of a cross between pure breeding lines, that the variances so partitioned can be considered precise estimates of environmental or additive genetic components (Falconer, 1960). The within family variance in a pure breeding line is a precise estimate of the environmental variance, as there is no genetic variance present.

The populations in this experiment do not represent pure breeding lines, although P. brachystemon is certain to be highly inbred. The information that can be obtained from an ANOVA comes therefore more from any changes which might be observed over the course of the experiment in the partitioning of the phenotypic variance between and within families. In theory inbreeding will tend to reduce the genetic component of the within family variance and increase the genetic component of the between family variance. Selection and random drift will tend to decrease the genetic components in both within and between family estimates. In the present

situation, where the genetic structure of the populations of the two species is unknown, there is no simple prediction of the results of the ANOVA; in fact, the results showed very little. For height at anthesis all three species groups had a significant between family component of variance in most populations (Appendix 1). There were no obvious trends which might have been expected, particularly the decrease in between family variance which might have been expected in response to selection.

Other changes in distribution

There was no evidence from the frequency histograms of height at anthesis in the various populations to suggest that there had been changes in the distribution other than the changes in mean and variance. That is, there was no evidence of changes in skewness or kurtosis, or development of bimodality in the distributions.

Days to anthesis (flowering time)

Means

As with height at anthesis, the mean flowering times for the selected populations differed significantly from the controls in most cases, the sole exception in this case being PCS early G_1 (Figure 14). High and low selection lines in all three species groups diverged, with the early lines flowering earlier than the controls, and the late lines flowering later. The divergence by the fifth cycle of selection was, in the case of PCO, 33.5% of the number of days to anthesis in the control (+20%, -13.5%) or 31.8 days (+19 days, -12.8 days). In PCS the divergence was 28.7% of the control (+16.3%, -12.4)

Figure 14. Mean number of days to anthesis (flowering time) in populations selected for flowering time. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

The following pairs of consecutive populations within lines did not differ significantly:

PCO early G_3 and G_4

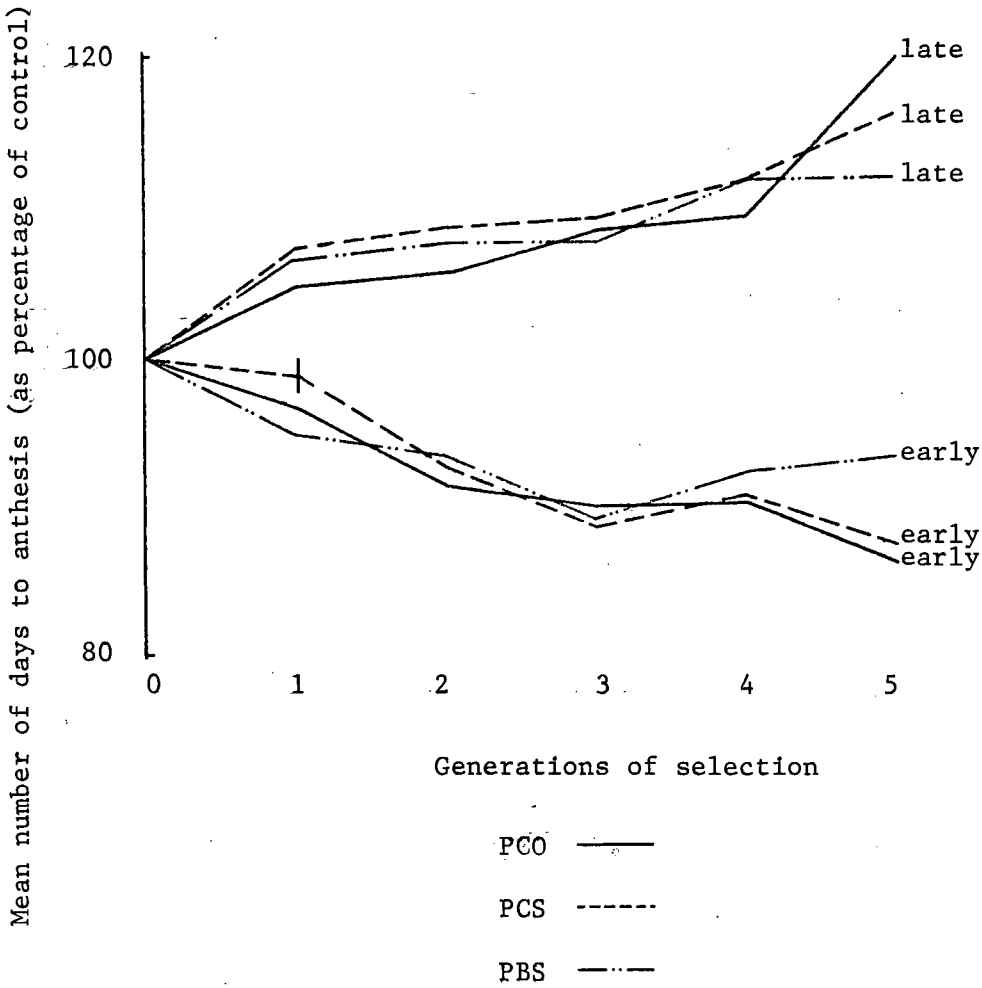
PCO late G_1 and G_2; G_3 and G_4

PCS early G_0 and G_1

PCS late G_1 and G_2; G_2 and G_3

PBS late G_1 and G_2; G_2 and G_3; G_4 and G_5

Figure 14.


Mean number of days to anthesis (as percentage of control)
120
100
80
0
1
2
3
4
5
late
late
late
early
early
early
Generations of selection
PCO
PCS
PBS

or 27.3 days (+15.5 days, -11.8 days). In PBS the divergence was 18.5% of the control (+12.2%, -6.3%) or 21.5 days (+14.2 days, -7.3 days).

The mean flowering times were also compared generation to generation within the selected lines, with the following populations proving not to be significantly different: PCS early G_1 vs. G_0, PCS late G_2 vs. G_1, G_3 vs. G_2, PCO late G_2 vs. G_1, and PBS late G_2 vs. G_1, G_3 vs. G_2.

Estimates of variability

Variances

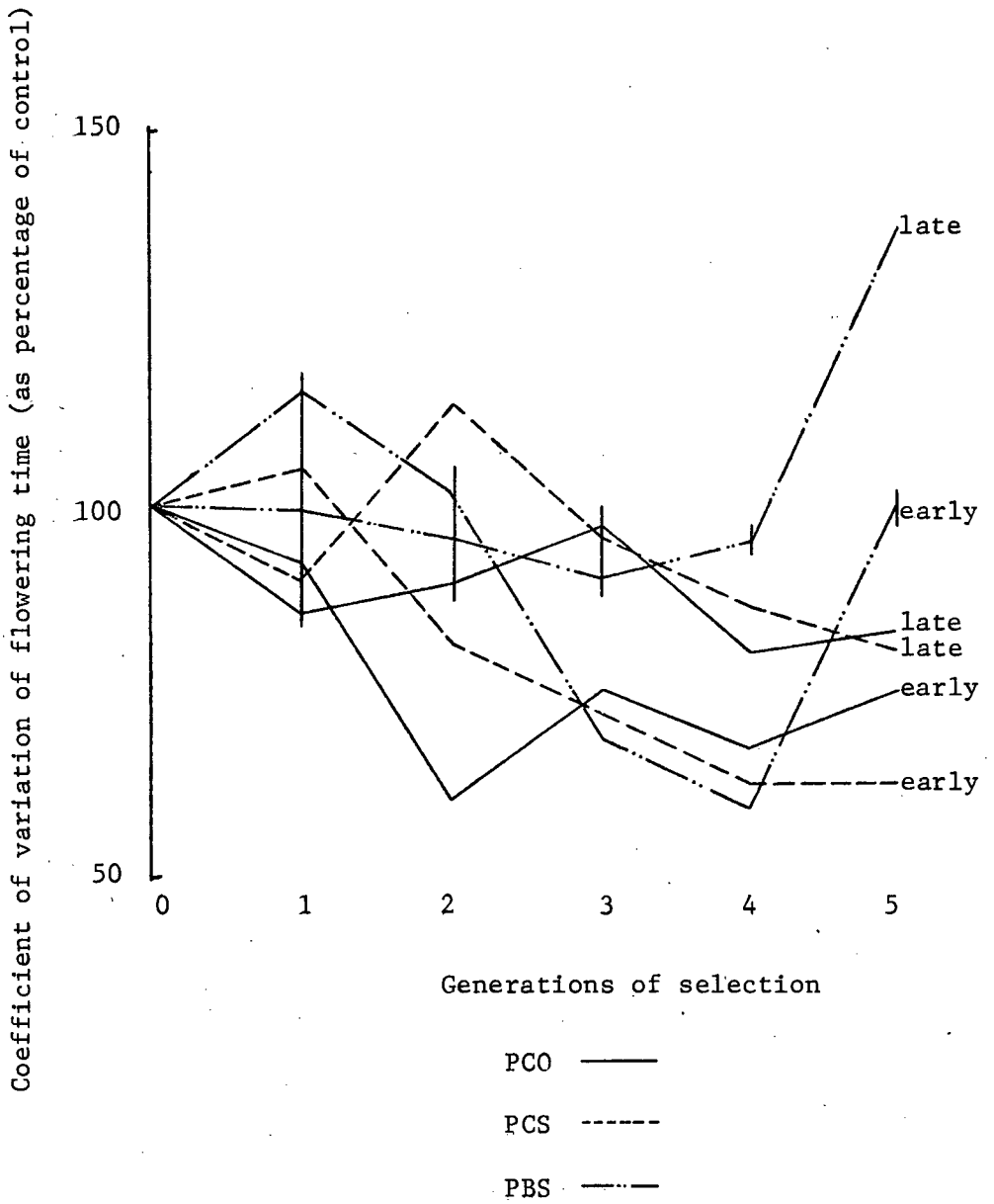
The variances in the populations were converted to coefficients of variation to remove scale effects. The coefficients of variation are presented graphically in Figure 15. The selected lines were compared to the controls by means of the modified F - test for coefficients of variation, and were found to be significantly different in 16 of the 30 populations, namely PCO early G_2 through G_5, PCO late G_4 and G_5, PCS early G_2 through G_5, PCS late G_2, G_4, and G_5, PBS early G_3 and G_4, and PBS late G_5. Of these, in all cases except PCS late G_2 and PBS late G_5 the variation was less in the selected lines than in the controls. The general trend in all six selected lines was towards a decrease in the coefficient of variation.

Heritabilities

The realised heritabilities (Table IV) again reveal the basic agreement between the PCO (b_c or $h^2 = 0.77$) and PCS ($b_c = 0.75$) lines. Plectritis brachystemon also has a reasonably large heritability for flowering time ($b_c = 0.49$). In all cases the standard deviation for the estimates is

Figure 15. Coefficients of variation for days to anthesis in populations selected for flowering time. Coefficients of variation are expressed as a percentage of the coefficients in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

Figure 15.


Coefficient of variation of flowering time (as percentage of control)
150
100
50
0
1
2
3
4
5
Generations of selection
late
early
late
late
early
early
PCO
PCS
PBS

considerably smaller than in the heritability estimates for height at anthesis.

The estimated heritabilities from parent-offspring regressions for flowering time (Table V) are comparable to the realised heritability estimates, with the two P. congesta control lines similar (PCO h^2 = 0.60, PCS h^2 = 0.72) and the P. brachystemon line slightly less (h^2 = 0.42), but still appreciable. Again, the reliability of the estimates is indicated by the goodness of fit of the regression lines to the data (r^2), which in this case shows a more reliable estimate of h^2 than did the regression for height at anthesis.

Components of variance

As with height at anthesis in lines selected for height, all the lines selected for flowering time showed a significant between family component of variance for flowering time in most populations. Once again, there was no significant trend in these parameters over the course of the experiment (Appendix 1).

Other changes in distribution

There was no evidence from the frequency histograms of flowering time in the populations selected for flowering time to suggest that there had been changes in the distribution other than changes in mean and variance. That is, there was no evidence of changes in skewness or kurtosis, or development of bimodality in the distributions.

Changes in the unselected characters during the experiment

The characters not under selection - days to emergence, height at anthesis in the lines selected for flowering time, number of nodes at anthesis, number of primary branches at anthesis, flowering time in lines selected for height at anthesis, and fruit production - were analysed in the same manner as the selected characters.

Means

Days to emergence

A number of populations departed significantly from the controls in terms of the mean number of days to emergence: PCO early G_1, PCO tall G_1, PCS early G_1, G_2, G_3, PCS late G_1, G_2, PBS early G_1, PBS tall G_1 and PBS short G_1 (Figure 16). In all groups selected for either height or flowering time, the G_5 means for days to emergence in the plus selected lines were greater than the means in the minus selected lines, with the exception of PCS selected for flowering time. However, a number of lines experienced reversals, with the plus selected line falling below the minus selected line: PCS anthesis G_1 and G_2, PCO height G_4, PCS height G_1, and PBS height G_1. There appears to be no regular trend in the changes in emergence date.

Height at anthesis (in lines selected for flowering time)

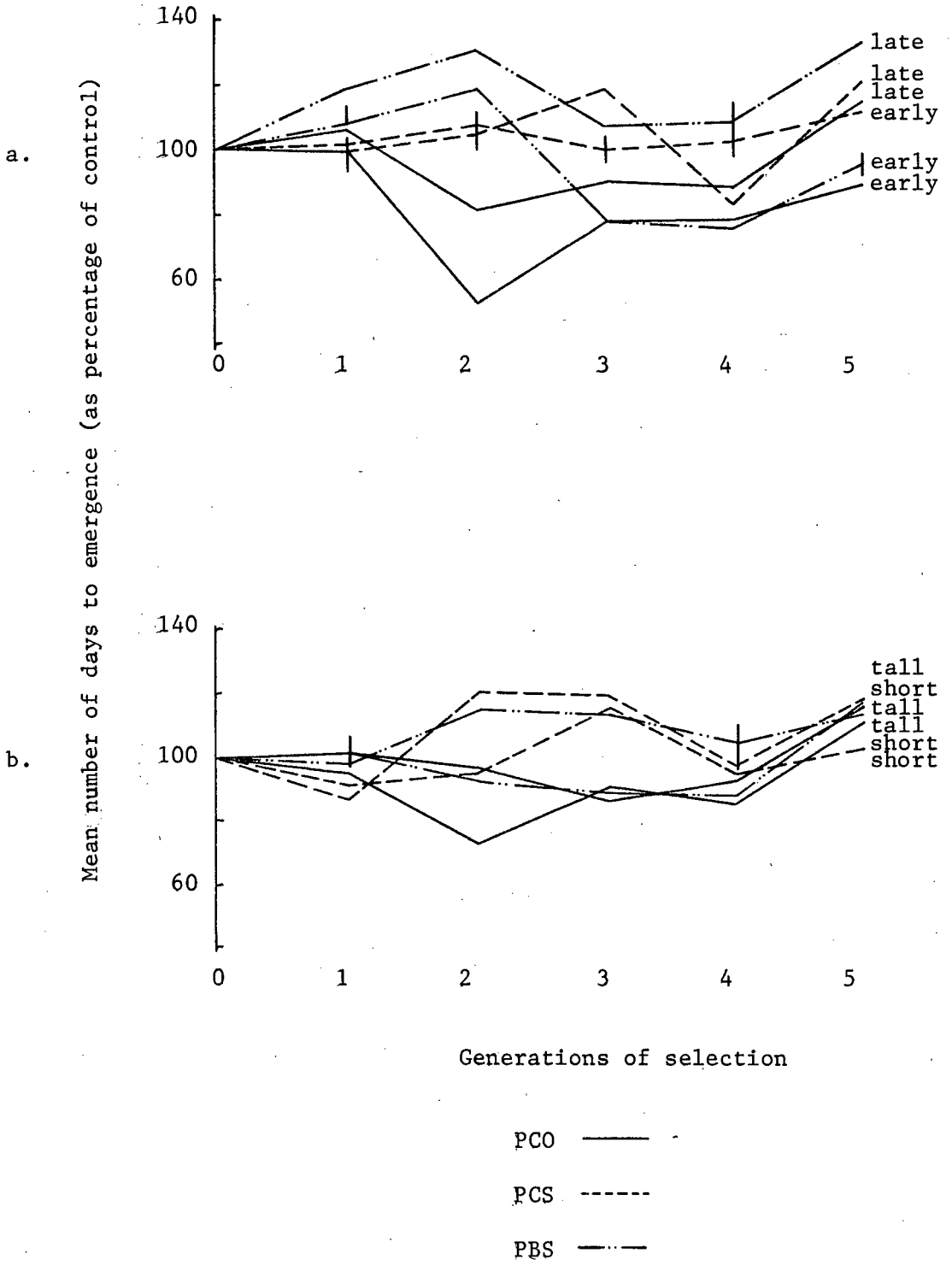
In the lines selected for flowering time, the mean heights differed significantly from the controls in PCO early G_2, G_3, PCO late G_1, G_2, PCS

Figure 16. Mean number of days to emergence in various populations. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

a. Mean number of days to emergence in populations selected for flowering time.

b. Mean number of days to emergence in populations selected for height at anthesis.

Figure 16.


a.
b.
140
100
60
0
1
2
3
4
5
late
late
late
early
early
early
tall
short
tall
tall
short
short
Mean number of days to emergence (as percentage of control)
Generations of selection
PCO
PCS
PBS

early G_1, PCS late G_3, PBS early G_2, G_3, and PBS late G_3 (Figure 17). The plus selected lines were all taller than the minus selected lines by G_5, but all lines were shorter than the control with the exception of PBS late. Both P. congesta lines experienced reversals in G_1. Again, there appear to be no long term trends in changes in height at anthesis in the lines selected for flowering time.

Nodes at anthesis

The mean number of nodes at anthesis departed significantly from the controls in all populations except PCO late G_1, PCO short G_1, G_3, PCO tall G_1, PCS short G_1, PCS tall G_2, and PBS tall G_1 (Figure 18). There was a strong trend toward divergence in lines selected for both height and flowering time, with all plus populations except PBS tall G_1 above the control and all minus populations except PBS short G_4 below it. The strong trend toward divergence is undoubtedly due in part to the same factors which lead to a strong correlation between the number of nodes at anthesis and flowering time (see Correlations below) as the divergence is more marked in lines selected for flowering time.

Primary branches at anthesis

The number of primary branches at anthesis in the selected lines showed large and somewhat erratic departures from the controls, the means being significantly different in all cases except PCO early G_2, PCO late G_1, G_3, PCO short G_2, PCO tall G_1, G_2, PCS early G_2, PCS late G_1, G_2, G_3, PCS short G_2, PCS tall G_1, PBS early G_2, PBS late G_1, PBS short G_2, and PBS tall

Figure 17. a. Mean height at anthesis in populations selected for flowering time. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

b. Mean number of days to anthesis in populations selected for height at anthesis. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

Figure 17.

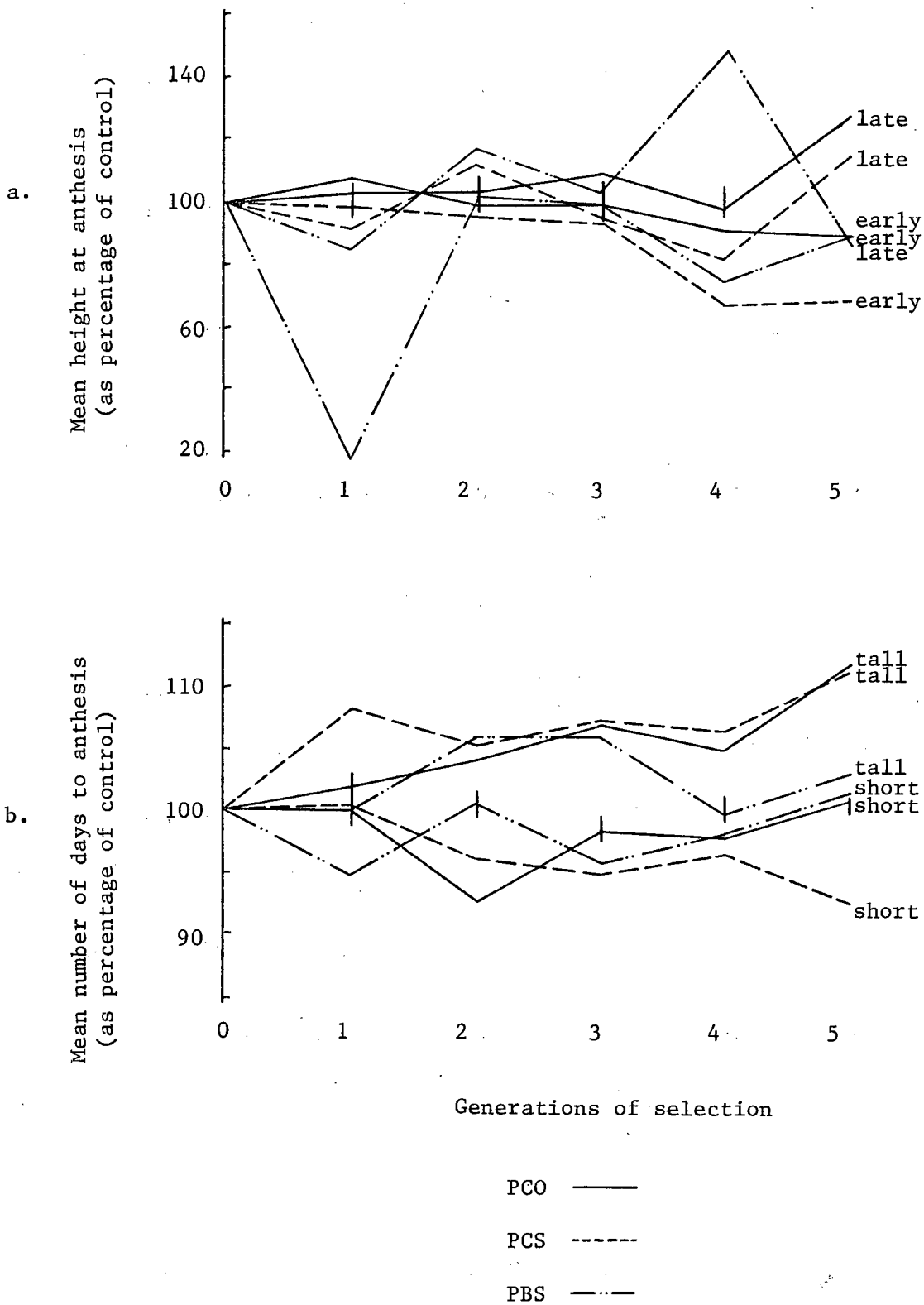
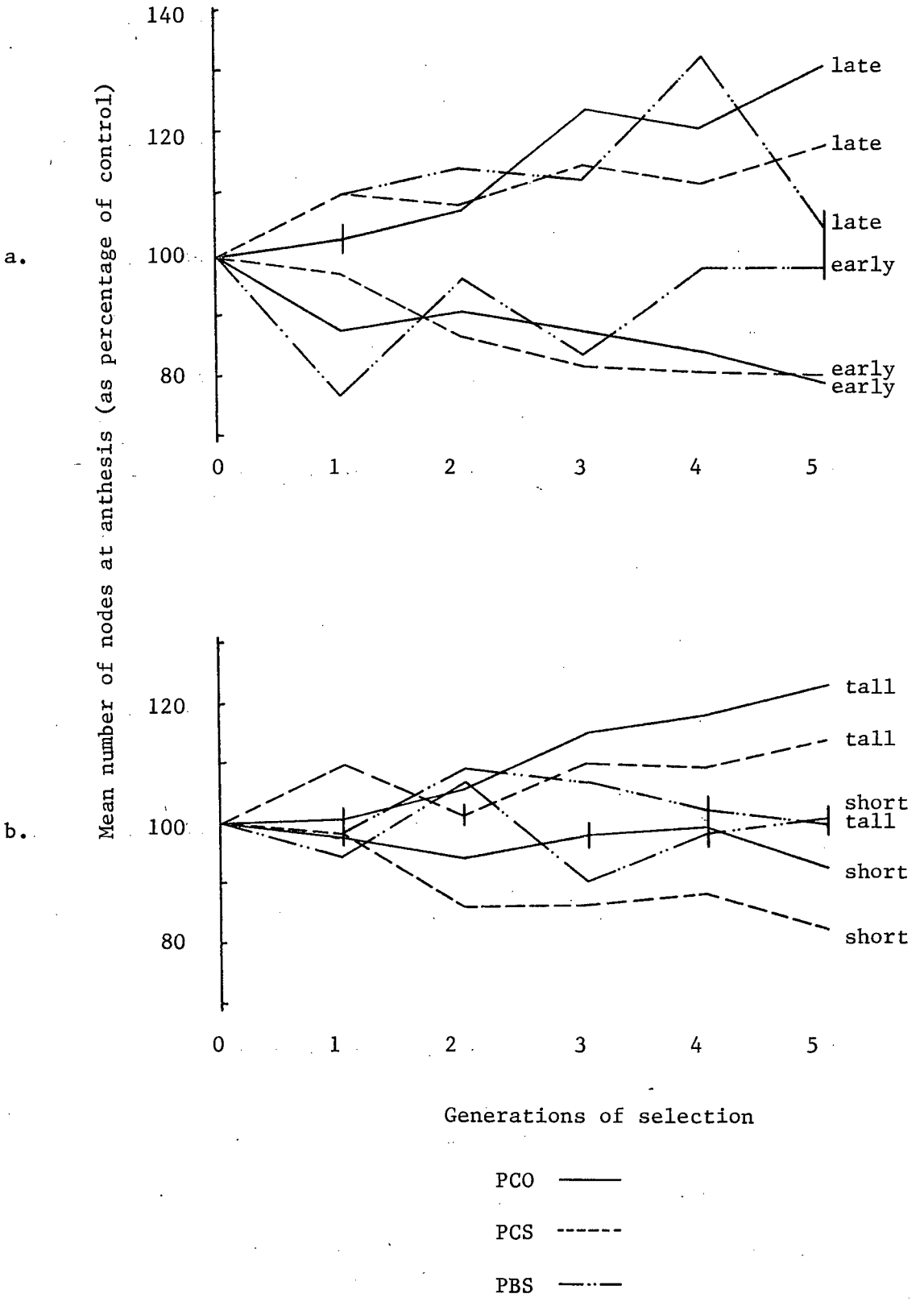

a.
Mean height at anthesis
(as percentage of control)
140
100
60
20
0
1
2
3
4
5
late
late
early
early
late
early
b.
Mean number of days to anthesis
(as percentage of control)
110
100
90
0
1
2
3
4
5
tall
tall
tall
short
short
short
Generations of selection
PCO
PCS
PBS

Figure 18. Mean number of nodes at anthesis in various populations. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

a. Mean number of nodes at anthesis in populations selected for flowering time.

b. Mean number of nodes at anthesis in populations selected for height at anthesis.

Figure 18.


a.
b.
Mean number of nodes at anthesis (as percentage of control)
140
120
100
80
0
1
2
3
4
5
late
late
late
early
early
early
tall
tall
short
tall
short
short
Generations of selection
PCO
PCS
PBS

G_3 (Figure 19). In most cases there was divergence, with the plus selected lines having more primary branches than the minus lines. A number of reversals were observed in the lines selected for height at anthesis (PBS G_1 and G_4, PCO G_3) and most lines fluctuated erratically, often above and below the controls in different generations. There may have been some effect of selection in the lines selected for flowering time, but otherwise there were no trends in the changes of the means. The fact that the selected lines seem to cycle up and down relative to the controls from generation to generation reflects changes in the controls rather than in the selected lines, and indicates the sensitivity of this character to changes in the environment from generation to generation.

Flowering time (in lines selected for height at anthesis)

Selection for height at anthesis appears to have had some effect on flowering time. All the selected lines have diverged somewhat, with all being significantly different from the controls except PCO short G_1, G_3, PCO tall G_1, PCS short G_1, PBS short G_2, and PBS tall G_1 (Figure 17). The strong correlation between flowering time and number of nodes at anthesis can be seen in the similarity between the changes in the means for the two in lines selected for height at anthesis (compare Figure 17 b with Figure 18 b).

Fruit production

Fruit production was a character whose measurement was subject to a great deal of error. As can be seen in Figure 20, the means in the selected lines departed significantly from the controls in many cases, the exceptions

Figure 19. Mean number of primary branches at anthesis in various populations. Means are expressed as a percentage of the means in the control lines. Populations which intersect the vertical lines did not differ significantly from the control population in the same generation (the vertical lines do not represent standard deviations).

a. Mean number of primary branches at anthesis in populations selected for flowering time.

b. Mean number of primary branches at anthesis in populations selected for height at anthesis.

Figure 19.

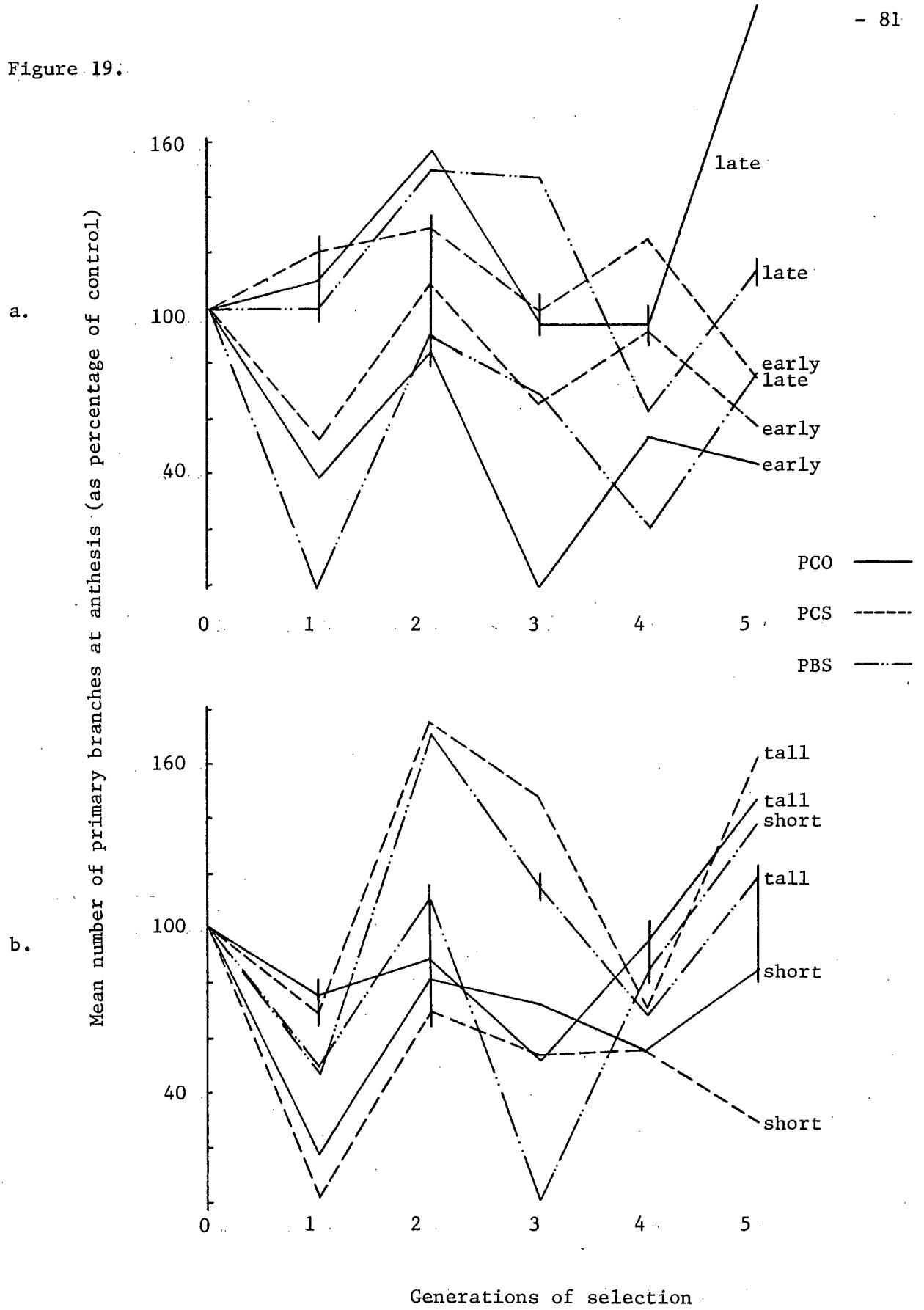
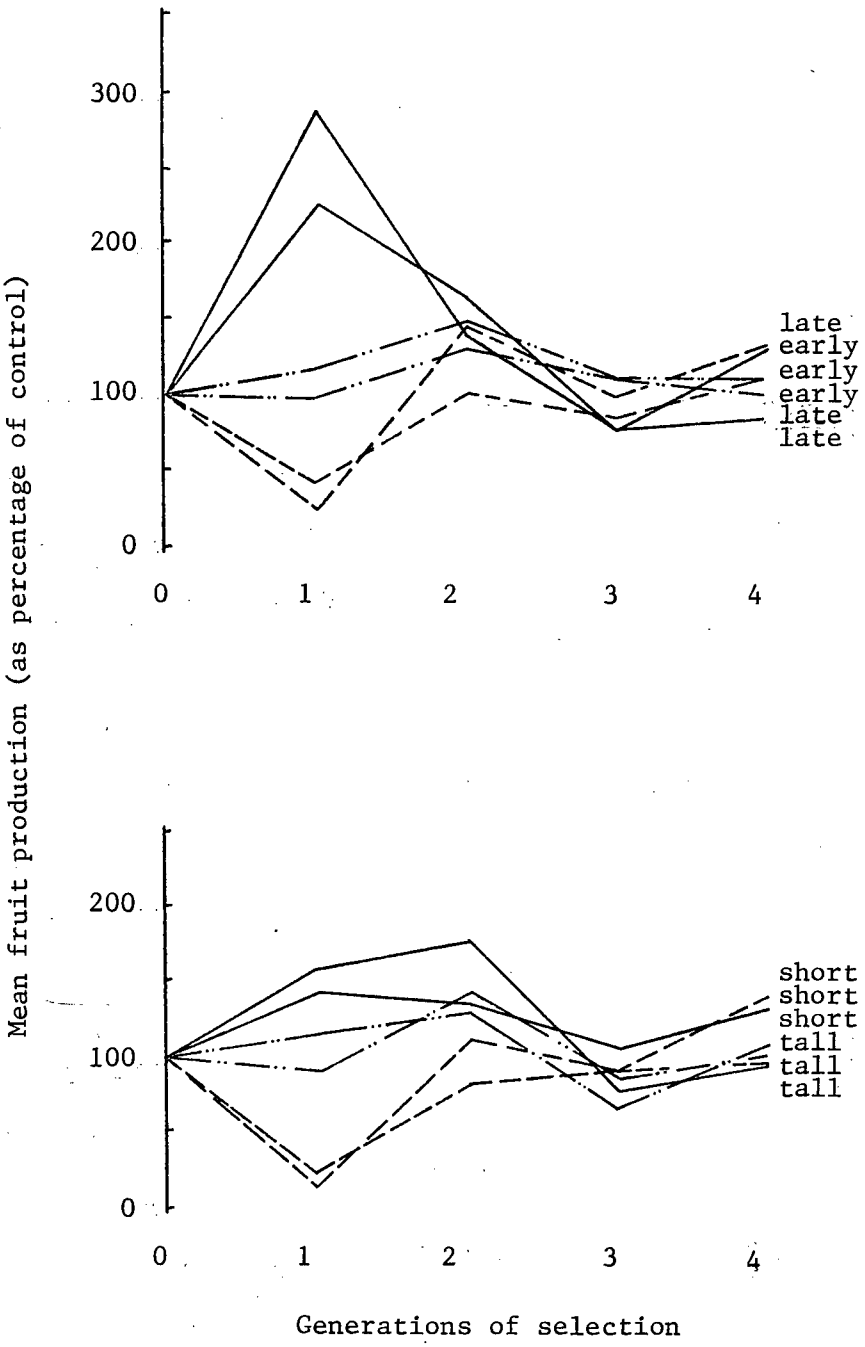

a.
b.
160
100
40
0
1
2
3
4
5
late
late
early
late
early
early
tall
tall
short
tall
short
short
PCO
PCS
PBS
Mean number of primary branches at anthesis (as percentage of control)
Generations of selection

Figure 20. Mean fruit production in various populations. Means are expressed as a percentage of the means in the control lines.

a. Mean fruit production in populations selected for flowering time. The following populations did not differ from the control in the same generation: PCO early G_3, PCO late G_4, PCS early G_2, G_3, G_4, PCS late G_1, G_3, PBS early G_1, G_3, and PBS late G_1, G_3, G_4.

b. Mean fruit production in populations selected for height at anthesis. The following populations did not differ from the control in the same generation: PCO short G_3, PCO tall G_3, G_4, PCS short G_1, G_3, PCS tall G_1, G_2, G_3, G_4, PBS short G_1, and PBS tall G_1, G_4.

Figure 20.


a.
b.
Mean fruit production (as percentage of control)
300
200
100
0
0
1
2
3
4
late
early
early
early
late
late
200
100
0
0
1
2
3
4
short
short
short
tall
tall
tall
Generations of selection
PCO
PCS
PBS

being PCO early G_3, PCO short G_3, PCO tall G_3, PCS early G_2, G_3, PCS late G_1, G_3, PCS short G_1, G_3, PCS tall G_1, G_2, G_3, PBS early G_1, G_3, PBS late G_1, G_3, PBS short G_1, and PBS tall G_1. It can also be seen that pairs of lines, plus and minus, wander erratically but together, suggesting that most of the movement is due to chance or error, and strongly influenced by the fruit production in the control lines.

Estimates of variability

Variances

The variances in the unselected characters, expressed as coefficients of variation, are presented in Appendix 2, and graphically for days to emergence and number of nodes at anthesis in Figures 21 and 22. Variation in days to emergence shows a general increase, with wide fluctuations, as does variation in the number of primary branches at anthesis. Height at anthesis in lines selected for flowering time is less variable in PCO and PCS early by G_5, and slightly more variable in PCS late and PBS. Variation in the number of nodes at anthesis tended to decrease, particularly in those lines selected for flowering time. Variation in flowering time in lines selected for height at anthesis decreased in the P. congesta lines, but fluctuated above and below the control in the P. brachystemon lines. Variation in fruit production also changed very erratically, reflecting the error inherent in the measurements.

Heritabilities

Figure 21. Coefficients of variation for number of days to emergence in the experimental populations. Coefficients of variation are expressed as a percentage of the coefficients of variation in the control lines.

a. Coefficients of variation for number of days to emergence in PCO populations.

b. Coefficients of variation for number of days to emergence in PCS populations.

c. Coefficients of variation for number of days to emergence in PBS populations.

Figure 21.

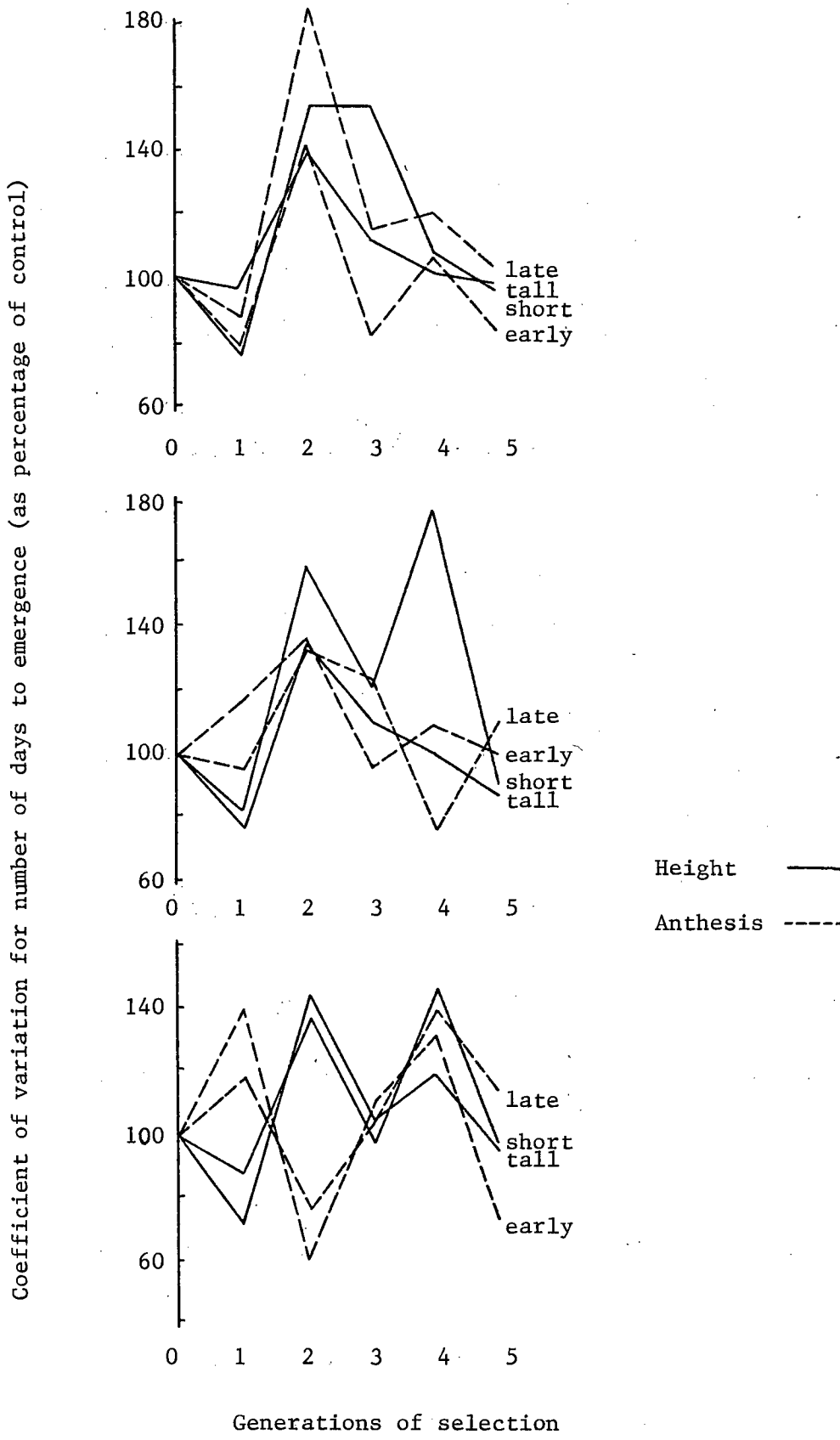

a. PCO
b. PCS
c. PBS
Coefficient of variation for number of days to emergence (as percentage of control)
180
140
100
60
0
1
2
3
4
5
late
tall
short
early
late
early
short
tall
late
short
tall
early
Height
Anthesis
Generations of selection

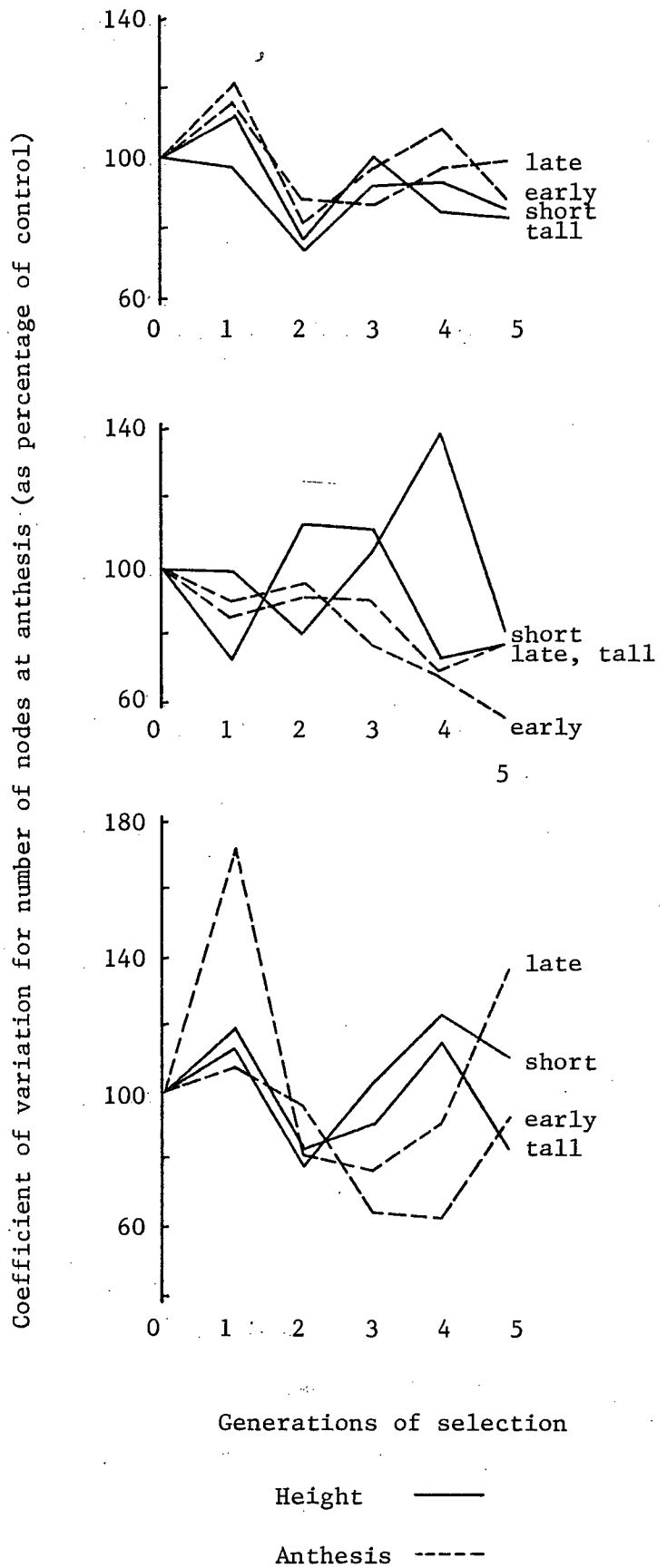
Figure 22. Coefficients of variation for number of nodes at anthesis in the experimental populations. Coefficients of variation are expressed as a percentage of the coefficients of variation in the control lines.

a. Coefficients of variation for number of nodes at anthesis in PCO populations.

b. Coefficients of variation for number of nodes at anthesis in PCS populations.

c. Coefficients of variation for number of nodes at anthesis in PBS populations.

Figure 22.


a. PCO
b. PCS
c. PBS
Coefficient of variation for number of nodes at anthesis (as percentage of control)
140
100
60
180
0
1
2
3
4
5
late
early
short
tall
short
late, tall
early
late
short
early
tall
Generations of selection
Height
Anthesis

There was only one estimate of heritability for the unselected characters from the experiment, as the realised heritability procedure is not applicable. The heritability estimates from parent-offspring regressions in the control lines for these characters are presented in Table VI. As indicated by the coefficients of determination, r^2, the fit of the regression line is quite poor in most cases. If the cases where r^2 is greater than 0.2 are considered alone, the following heritabilities may be estimated. For days to emergence, $h^2 = 0.49$ in PCO. For nodes at anthesis, $h^2 = 0.55$ in PCO, 0.57 in PCS, and 0.28 in PBS; these values are comparable and somewhat intermediate to the estimated heritabilities for the selected characters. Only PBS has reasonably precise estimates for the number of primary branches, $h^2 = 0.29$, and none of the lines provided a reliable estimate for the heritability of fruit production.

Components of variance

There were significant between family components of variance in all the unselected characters in all three species groups and most populations (Appendix 1). As with the selected characters, there were no consistent trends over the course of the experiment, and nothing to suggest changes due to selection in the partitioning of the total variance between and within families.

Other changes in distribution

As with the selected characters, there was no evidence from the frequency histograms of the unselected characters to suggest any changes in distributions other than the changes in mean and variance.

Table VI. Heritabilities from parent-offspring regressions, unselected characters.

	PCO control		PCS control		PBS control	
	h^2	r^2	h^2	r^2	h^2	r^2
Days to emergence						
G_2	.68	.65	.43	.14	-.16	.026
G_3	.09	.0058	.18	.03	-.21	.056
G_4	.31	.20	.12	.018	.32	.14
G_5	.0007	.0000	.28	.082	.14	.10
$\bar{x}$	.49					
Nodes at anthesis						
G_2	.71	.48	.43	.20	-.066	.0084
G_3	.48	.48	.73	.53	.13	.052
G_4	.46	.39	.49	.46	.28	.25
G_5	.17	.059	.65	.80	-.13	.087
$\bar{x}$	.55		.57		.28	
Primary branches at anthesis						
G_2	-.05	.0043	.081	.02	.22	.069
G_3	-.27	.092	.34	.22	-.29	.14
G_4	.076	.02	.24	.22	.20	.18
G_5	-.12	.035	.38	.18	-.13	.053
$\bar{x}$			.29			

Table VI, continued.

	PCO control		PCS control		PBS control	
	h^2	r^2	h^2	r^2	h^2	r^2
Fruit production						
G_2	.05	.0052	-.015	.0009	.15	.14
G_3	-.10	.055	.11	.07	-.034	.0045
G_4	.15	.099	.11	.023	-.083	.011
G_5	.079	.02	-.11	.055	-.033	.0059

The effects of selection on correlations among the measured characters

The correlation between height at anthesis and flowering time, the characters under selection.

The correlation between the selected characters, height at anthesis and flowering time, was initially significant and positive in all three species groups (Figure 23). It decreased more or less steadily towards no correlation in the PBS lines, even becoming significantly negative in two cases (PBS tall G_3 and PBS short G_4). There was some decrease evident in the P. congesta lines, particularly in the third cycle, G_3, when several of the populations showed a significant negative correlation, but by G_4 the correlations were mostly positive again, and it is difficult to discern any trend from the first five generations of selection.

Other correlations

The other correlations can be divided into three broad groups. In some cases, the correlations differed between the P. congesta lines and the P. brachystemon lines. In the correlations between height at anthesis and number of primary branches (Figure 24), number of nodes and number of primary branches (Figure 25), and height at anthesis and fruit production (Figure 26) the correlations in the PBS lines were strong and positive, while the correlations in the PCO and PCS lines were mostly not significant and not consistently positive or negative.

In some cases the correlations were essentially similar in all three species groups and mostly not significant, or when significant not

Figure 23. Correlations between height at anthesis and flowering time. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 23.

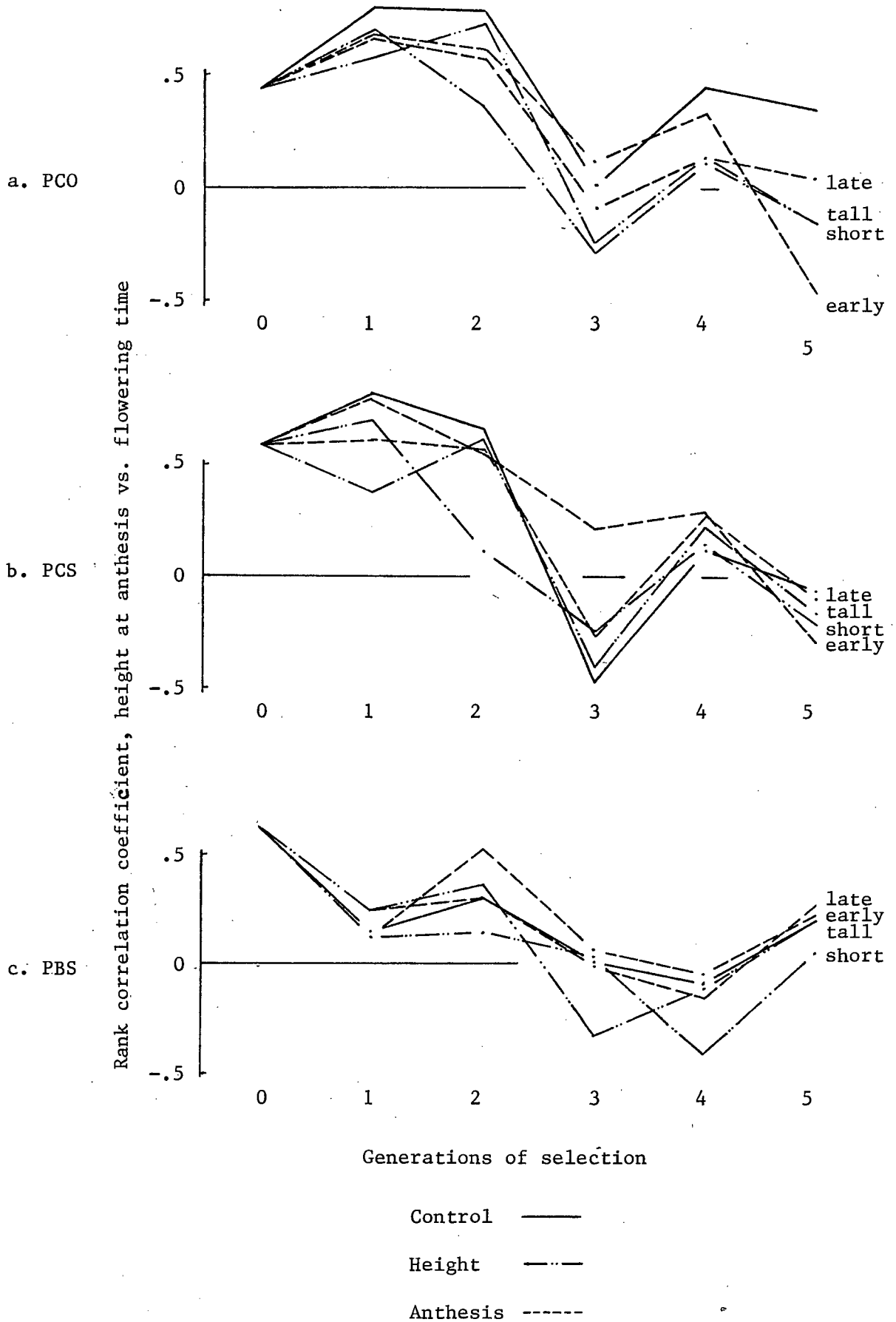

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
5
late
tall
short
early
Rank correlation coefficient, height at anthesis vs. flowering time
Generations of selection
Control
Height
Anthesis

Figure 24. Correlations between height at anthesis and number of primary branches at anthesis. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 24.

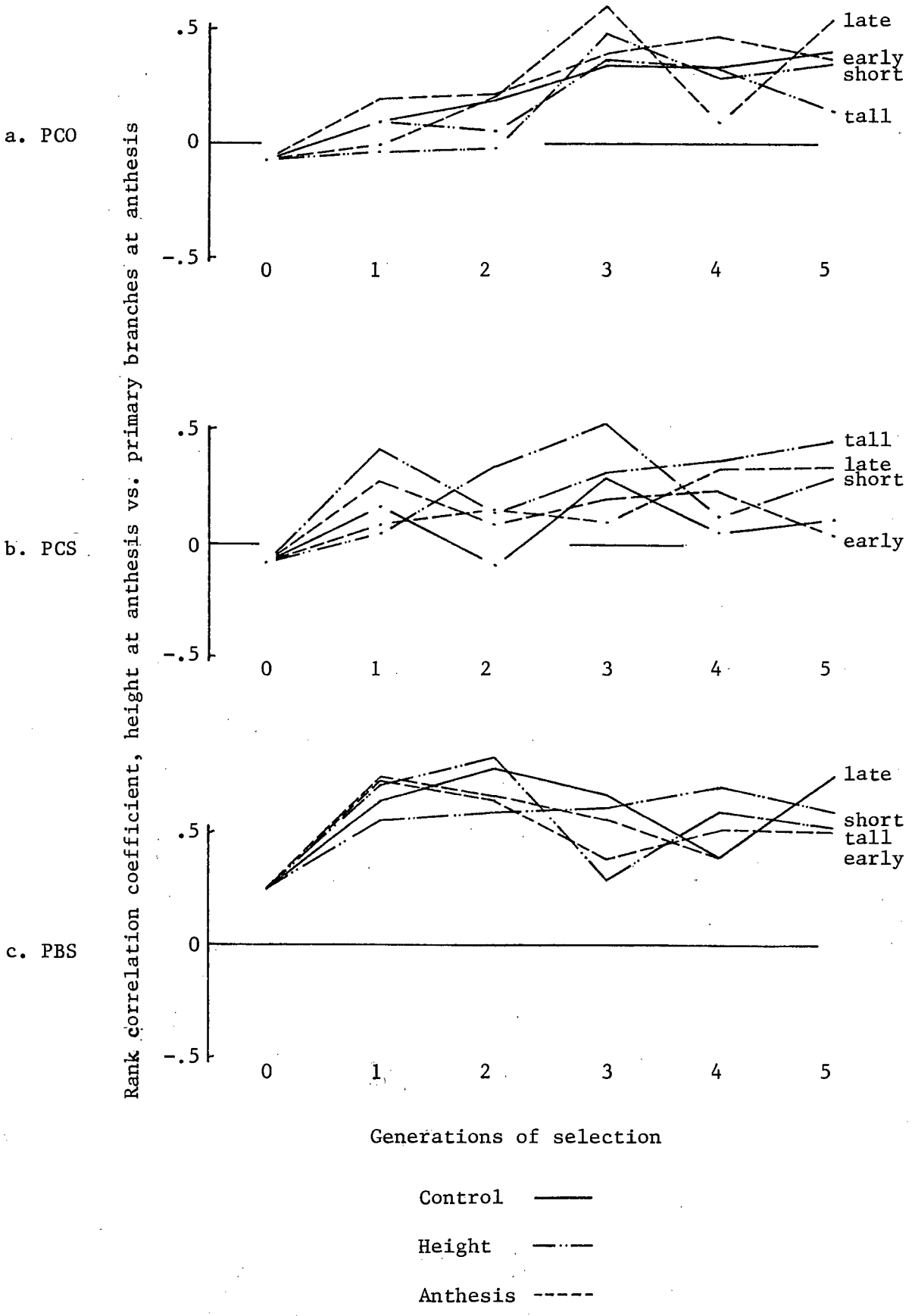

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
5
late
early
short
tall
tall
late
short
early
late
short
tall
early
Rank correlation coefficient, height at anthesis vs. primary branches at anthesis
Generations of selection
Control
Height
Anthesis

Figure 25. Correlations between number of nodes at anthesis and number of primary branches at anthesis. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 25.

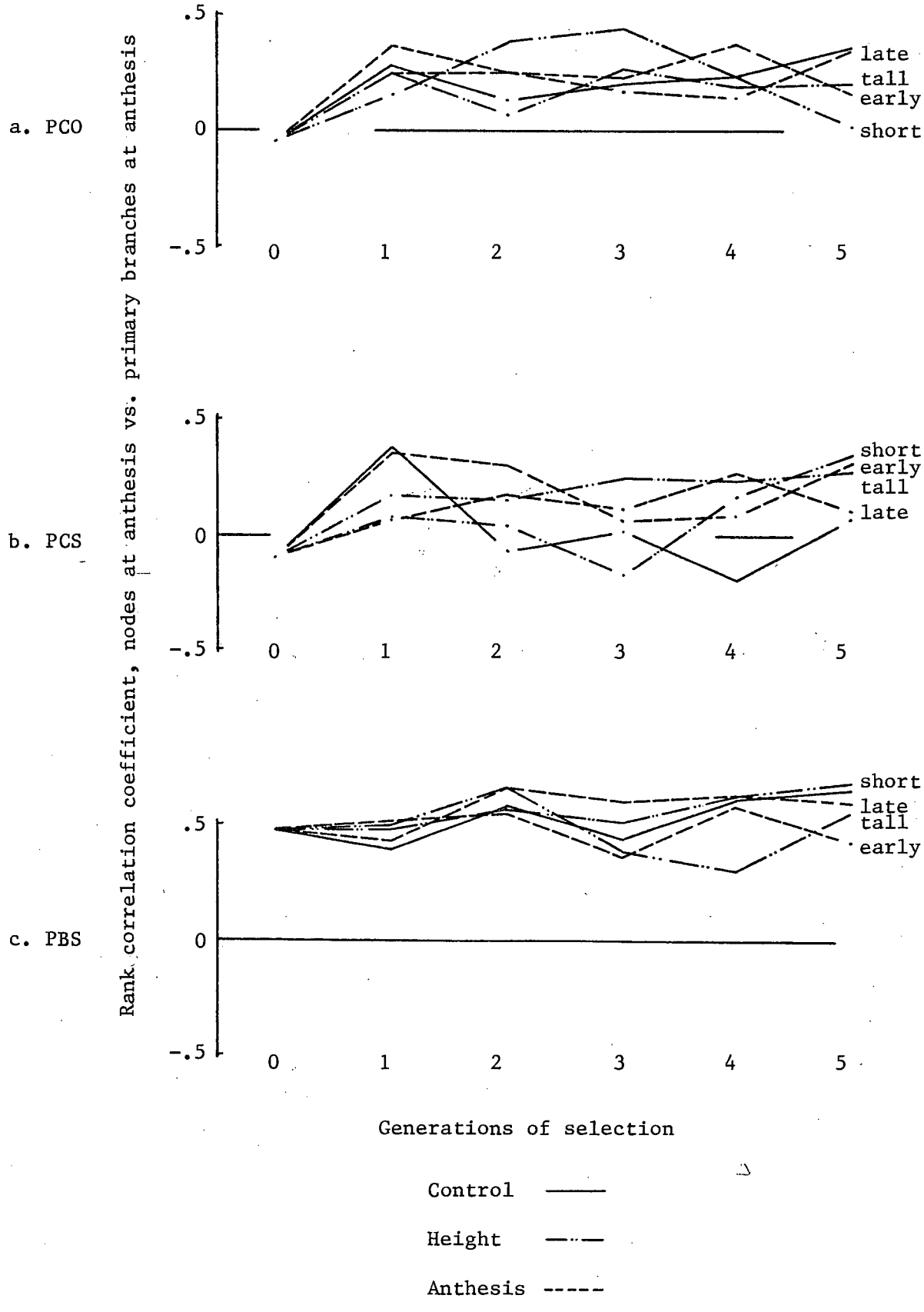

a. PCO
b. PCS
c. PBS
Rank correlation coefficient, nodes at anthesis vs. primary branches at anthesis
.5
0
-.5
0
1
2
3
4
5
late
tall
early
short
short
early
tall
late
short
late
tall
early
Generations of selection
Control
Height
Anthesis

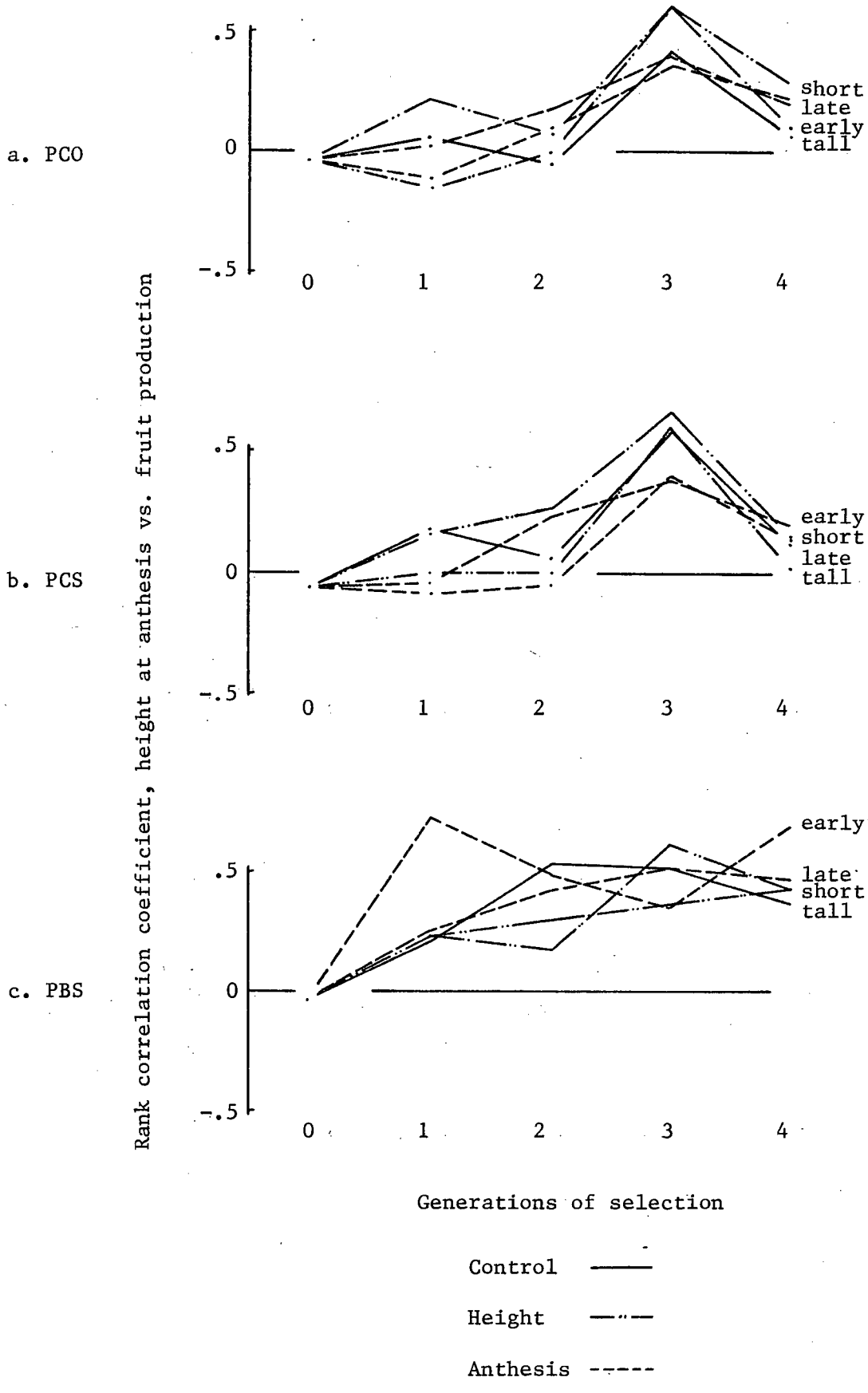
Figure 26. Correlations between height at anthesis and fruit production. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 26.


a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
short
late
early
tall
early
short
late
tall
early
late
short
tall
Rank correlation coefficient, height at anthesis vs. fruit production
Generations of selection
Control
Height
Anthesis

consistently positive or negative within a species group. For example, correlations between days to emergence and height at anthesis (Figure 27), days to emergence and number of nodes at anthesis (Figure 28), number of nodes at anthesis and fruit production (Figure 29), and primary branches and flowering time (Figure 30) fluctuate between being significant and positive, non-significant, and significant and negative, often within the same line (for example, primary branches vs. flowering time in PBS short shows this kind of pattern).

Finally, some of the correlations were for the most part significant in all three species groups, and remained so throughout the experiment. This is the case with negative correlations between days to emergence and number of primary branches (Figure 31), days to emergence and fruit production (Figure 32), and flowering time and fruit production (Figure 33). Significant positive correlations were observed consistently between days to emergence and flowering time, with the exception of G_4 and G_5 in the PBS lines, in which the correlation disappeared (Figure 34), between number of nodes and flowering time (Figure 35), number of primary branches and fruit production (Figure 36), and height at anthesis and number of nodes, with the exception of some of the populations in G_3, in which the correlation dropped (Figure 37).

It must be remembered that these are phenotypic, rather than genotypic, correlations, and as such are subject to environmental effects. Nevertheless, there does not appear to have been any change in any of the correlations between the various characters which could be attributed to the effects of selection, except perhaps in the case of the correlations between the selected characters.

Figure 27. Correlations between number of days to emergence and height at anthesis. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 27.

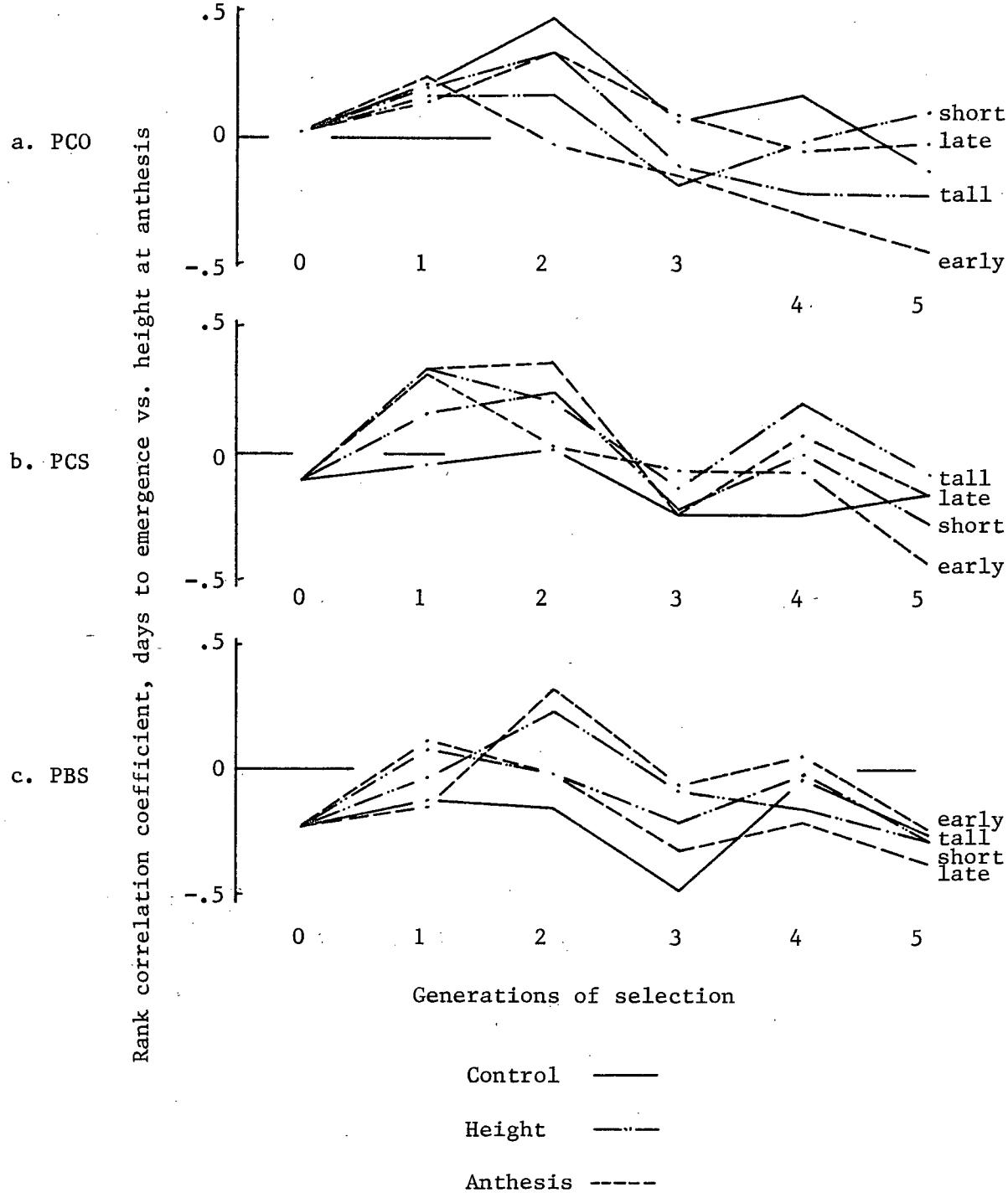

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
5
short
late
tall
early
tall
late
short
early
early
tall
short
late
Rank correlation coefficient, days to emergence vs. height at anthesis
Generations of selection
Control
Height
Anthesis

Figure 28. Correlations between number of days to emergence and number of nodes at anthesis. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlatio was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 28.

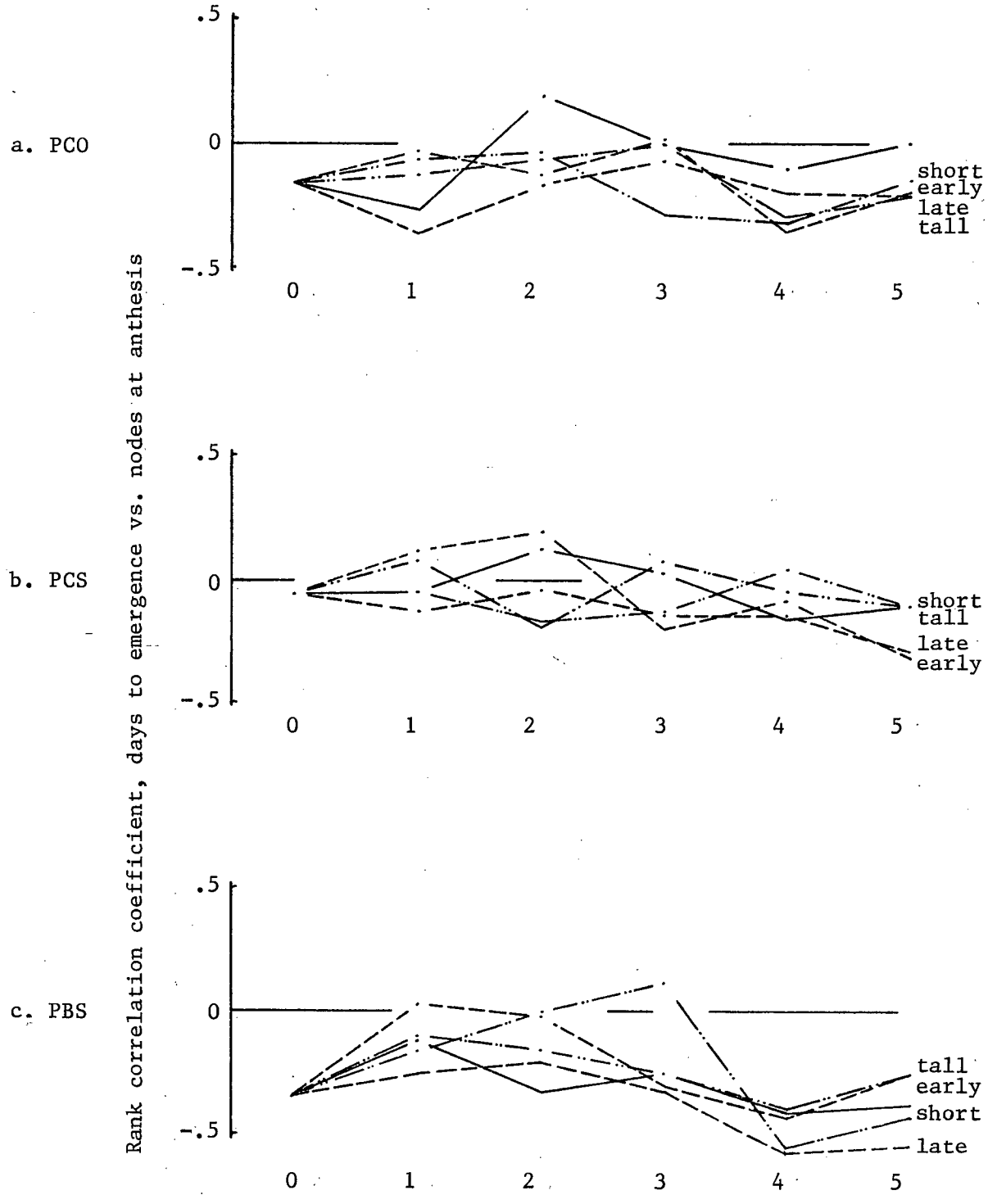

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
5
short
early
late
tall
short
tall
late
early
tall
early
short
late
Rank correlation coefficient, days to emergence vs. nodes at anthesis
Generations of selection
Control
Height
Anthesis

Figure 29. Correlations between number of nodes at anthesis and fruit production. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 29.

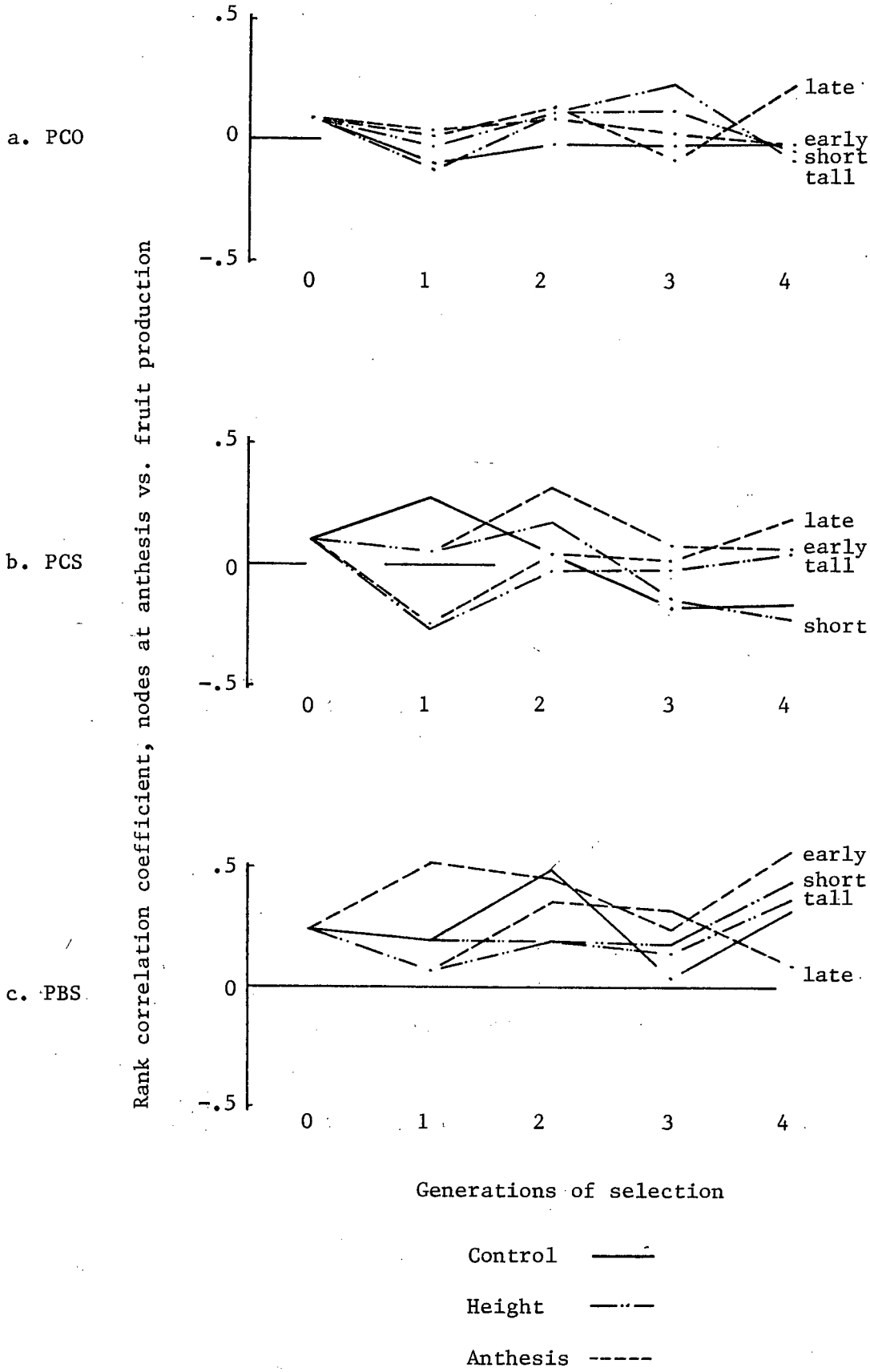

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
late
early
short
tall
Rank correlation coefficient, nodes at anthesis vs. fruit production
Generations of selection
Control
Height
Anthesis

Figure 30. Correlations between number of primary branches at anthesis and flowering time. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 30.

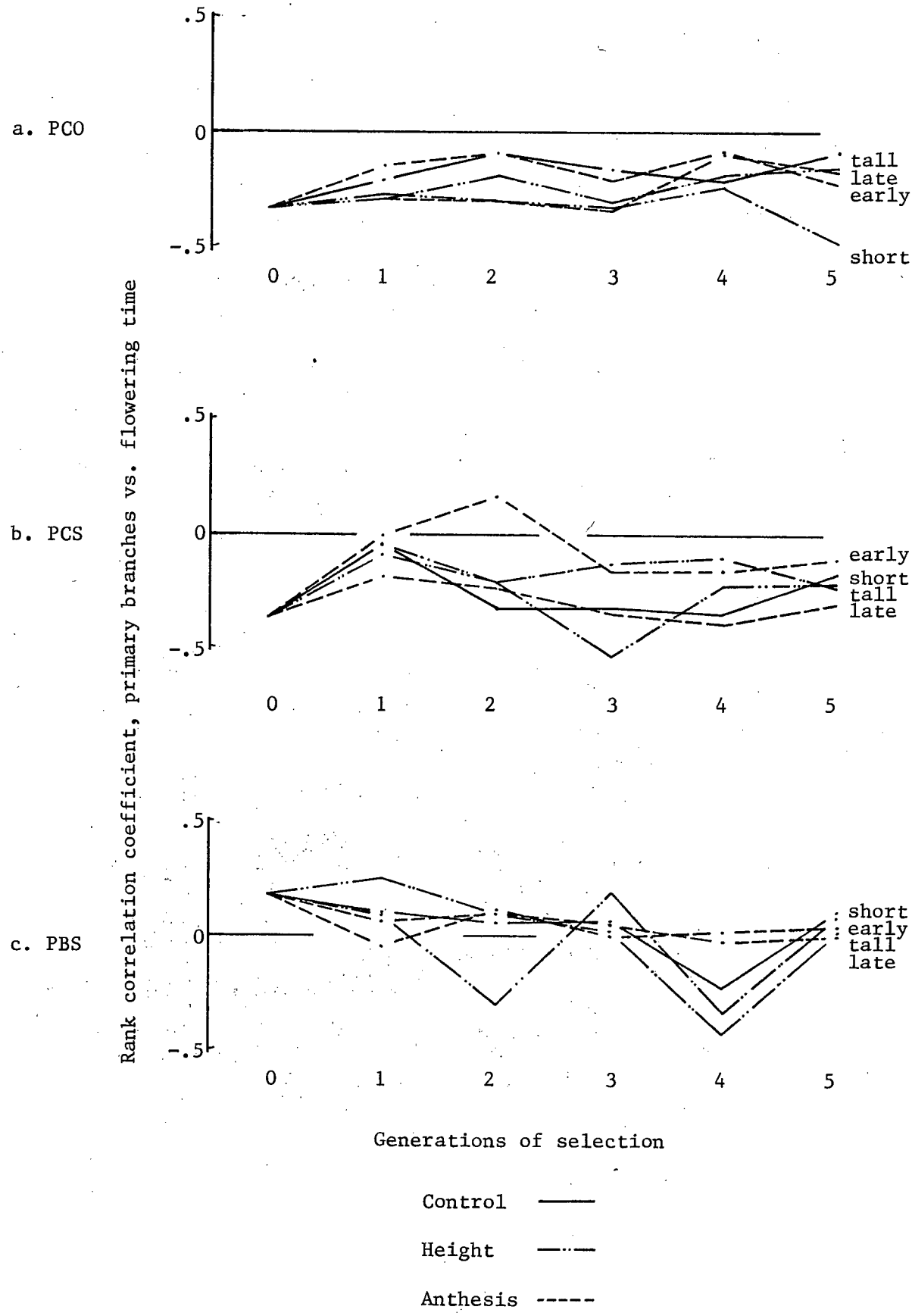

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
5
tall
late
early
short
Rank correlation coefficient, primary branches vs. flowering time
Generations of selection
Control
Height
Anthesis

Figure 31. Correlations between number of days to emergence and number of primary branches at anthesis. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 31.

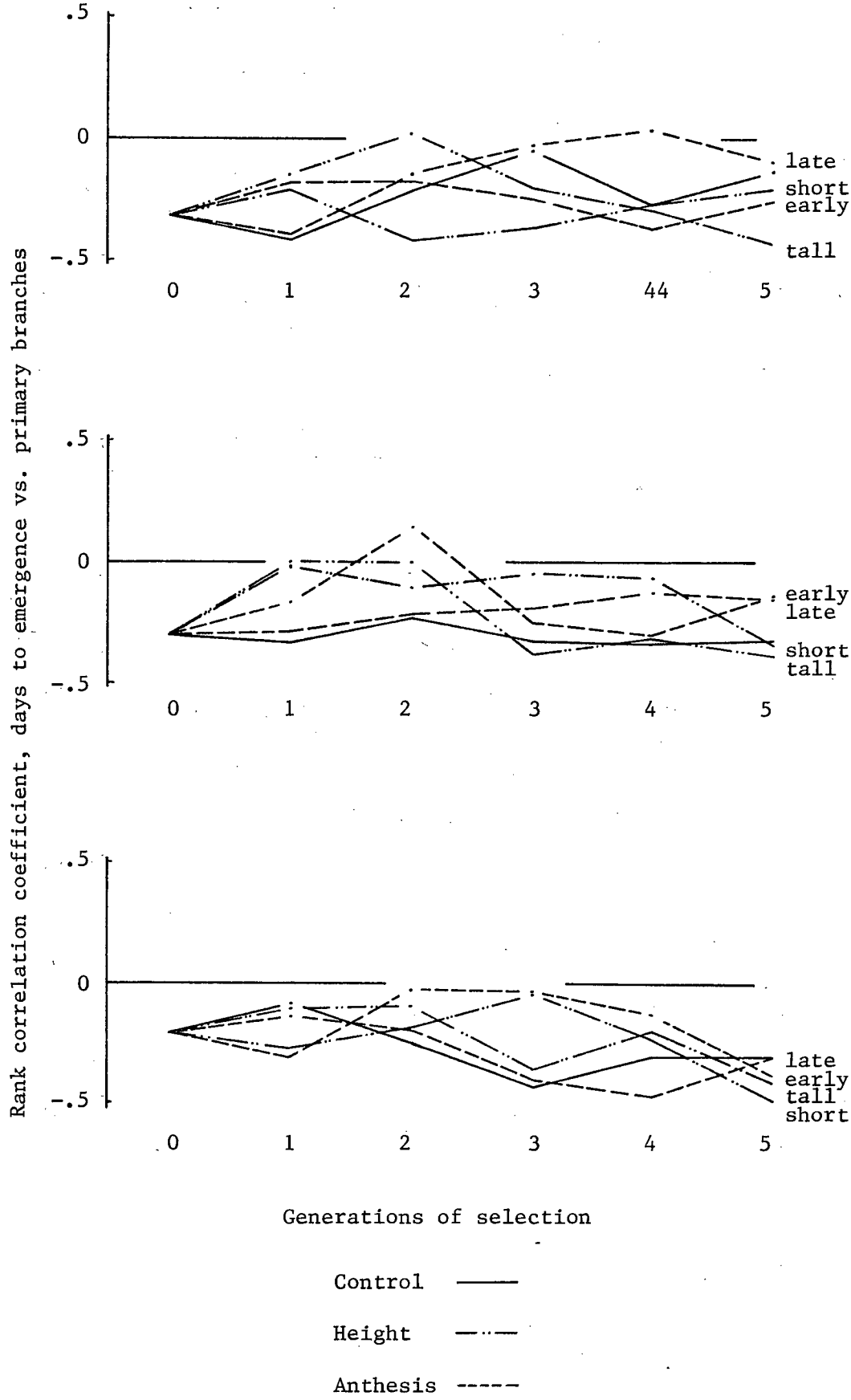

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
44
4
5
late
short
early
tall
Rank correlation coefficient, days to emergence vs. primary branches
Generations of selection
Control
Height
Anthesis

Figure 32. Correlations between number of days to emergence and fruit production. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations

Figure 32.

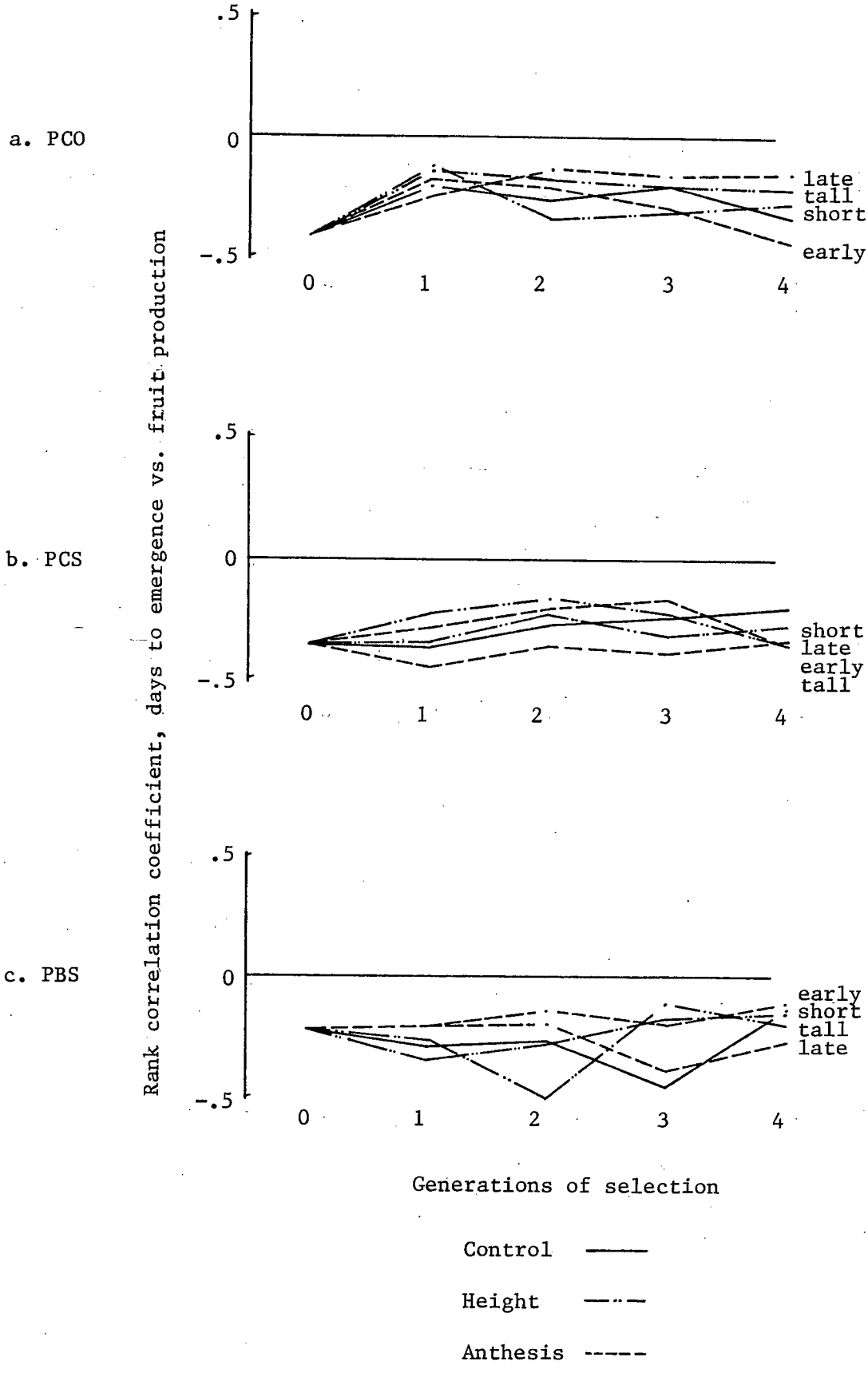

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
late
tall
short
early
short
late
early
tall
early
short
tall
late
Rank correlation coefficient, days to emergence vs. fruit production
Generations of selection
Control
Height
Anthesis

Figure 33. Correlations between flowering time and fruit production. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 33.

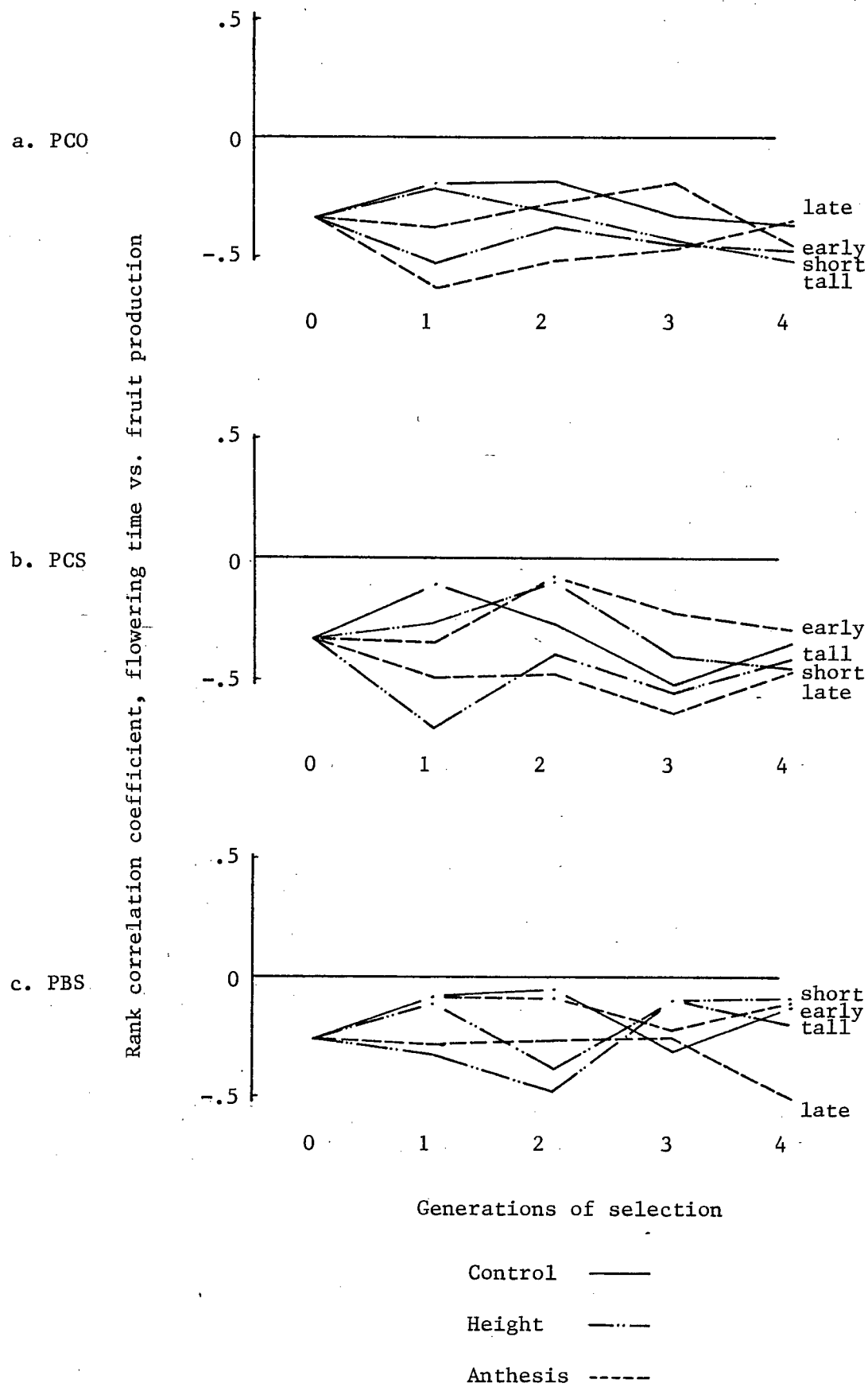

a. PCO
b. PCS
c. PBS
Rank correlation coefficient, flowering time vs. fruit production
.5
0
-.5
0
1
2
3
4
late
early
short
tall
early
tall
short
late
short
early
tall
late
Generations of selection
Control
Height
Anthesis

Figure 34. Correlations between number of days to emergence and flowering time. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 34.

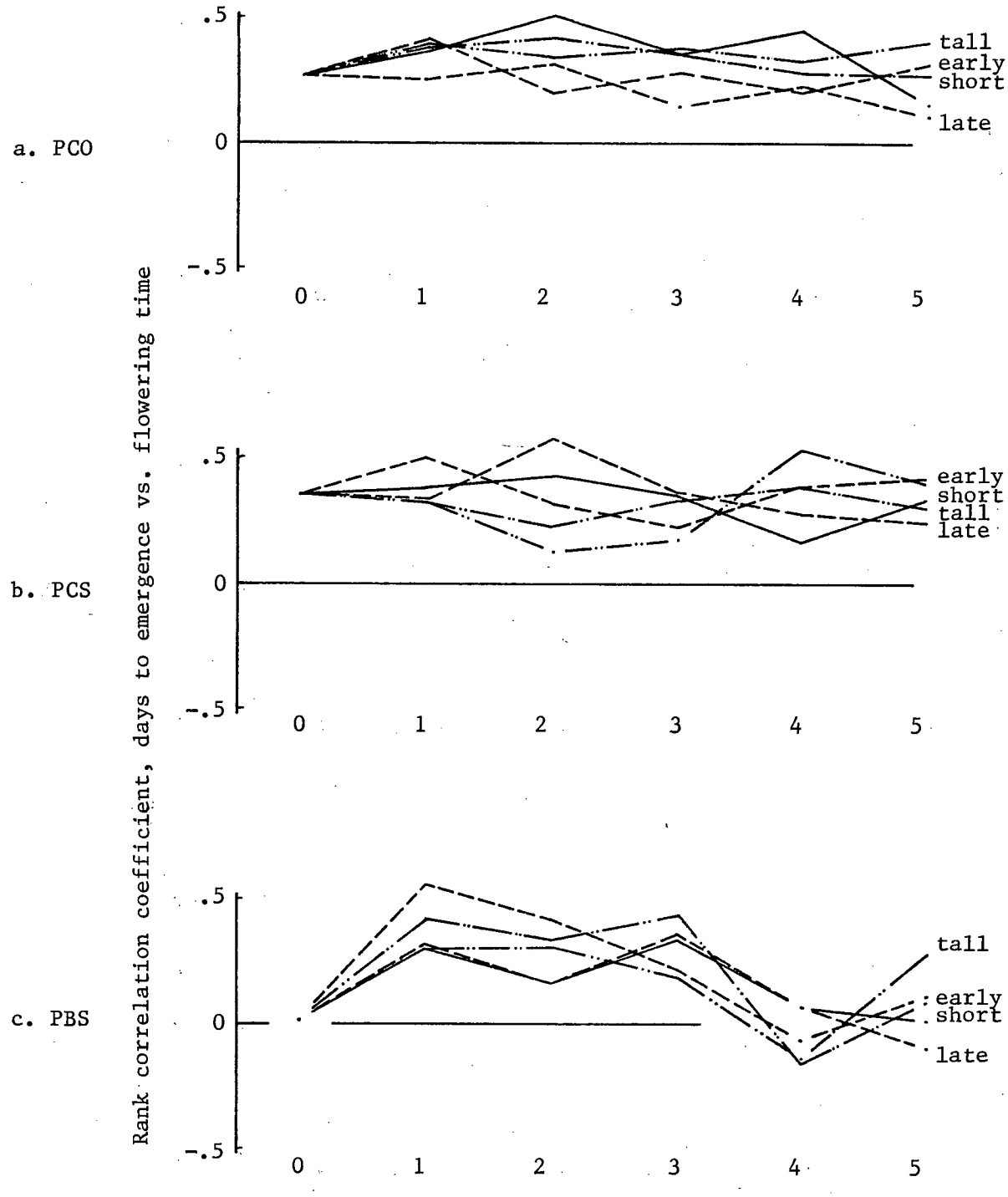

a. PCO
b. PCS
c. PBS
.5
0
-.5
0
1
2
3
4
5
tall
early
short
late
Rank correlation coefficient, days to emergence vs. flowering time
Generations of selection
Control
Height
Anthesis

Figure 35. Correlations between number of nodes at anthesis and flowering time. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

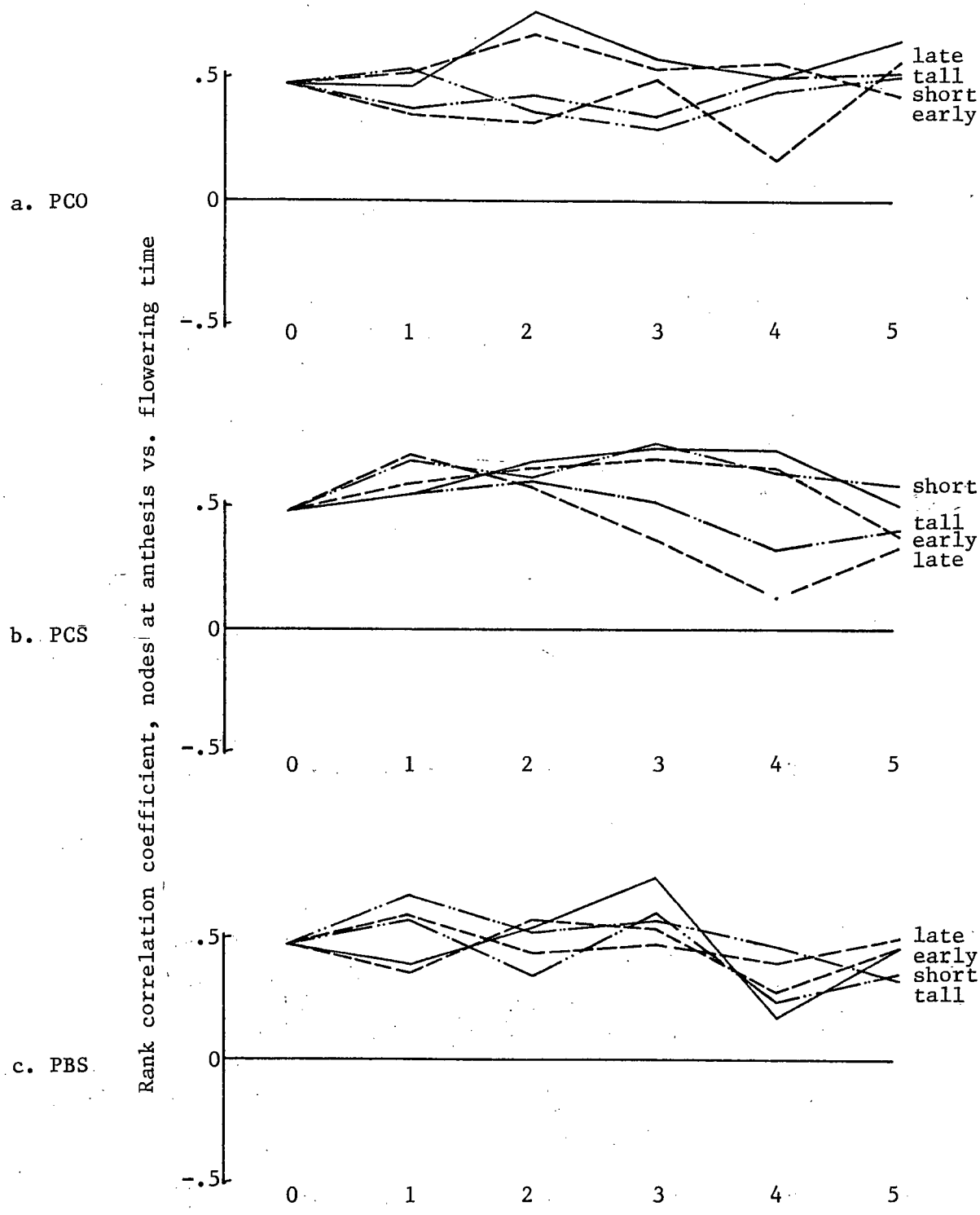

a. PCO
b. PCS
c. PBS
Rank correlation coefficient, nodes at anthesis vs. flowering time
.5
0
-.5
0
1
2
3
4
5
late
tall
short
early
short
tall
early
late
late
early
short
tall
Generations of selection
Control
Height
Anthesis

Figure 36. Correlations between number of primary branches at anthesis and fruit production. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 36.

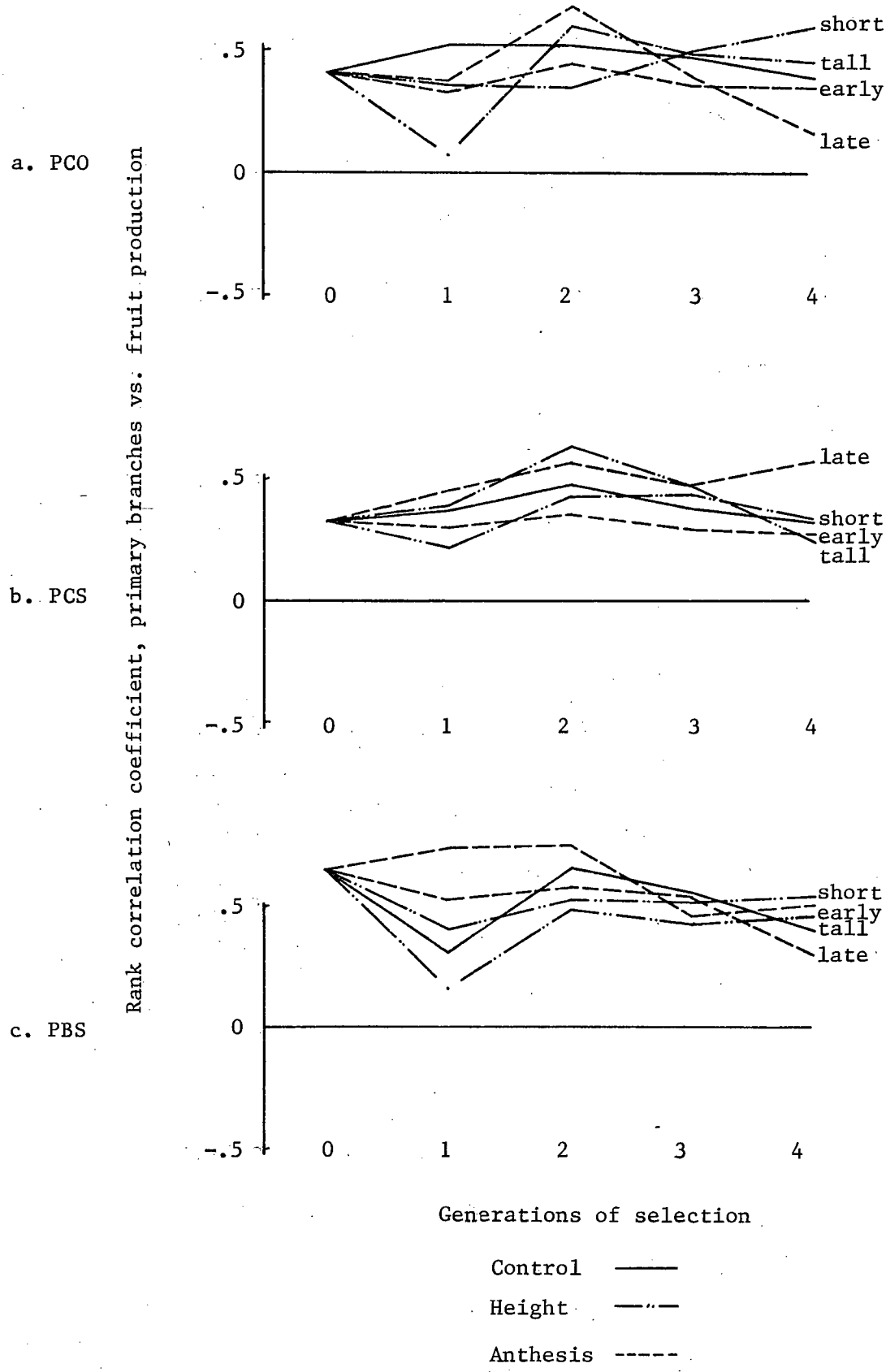

a. PCO
b. PCS
c. PBS
Rank correlation coefficient, primary branches vs. fruit production
.5
0
-.5
0
1
2
3
4
short
tall
early
late
Generations of selection
Control
Height
Anthesis

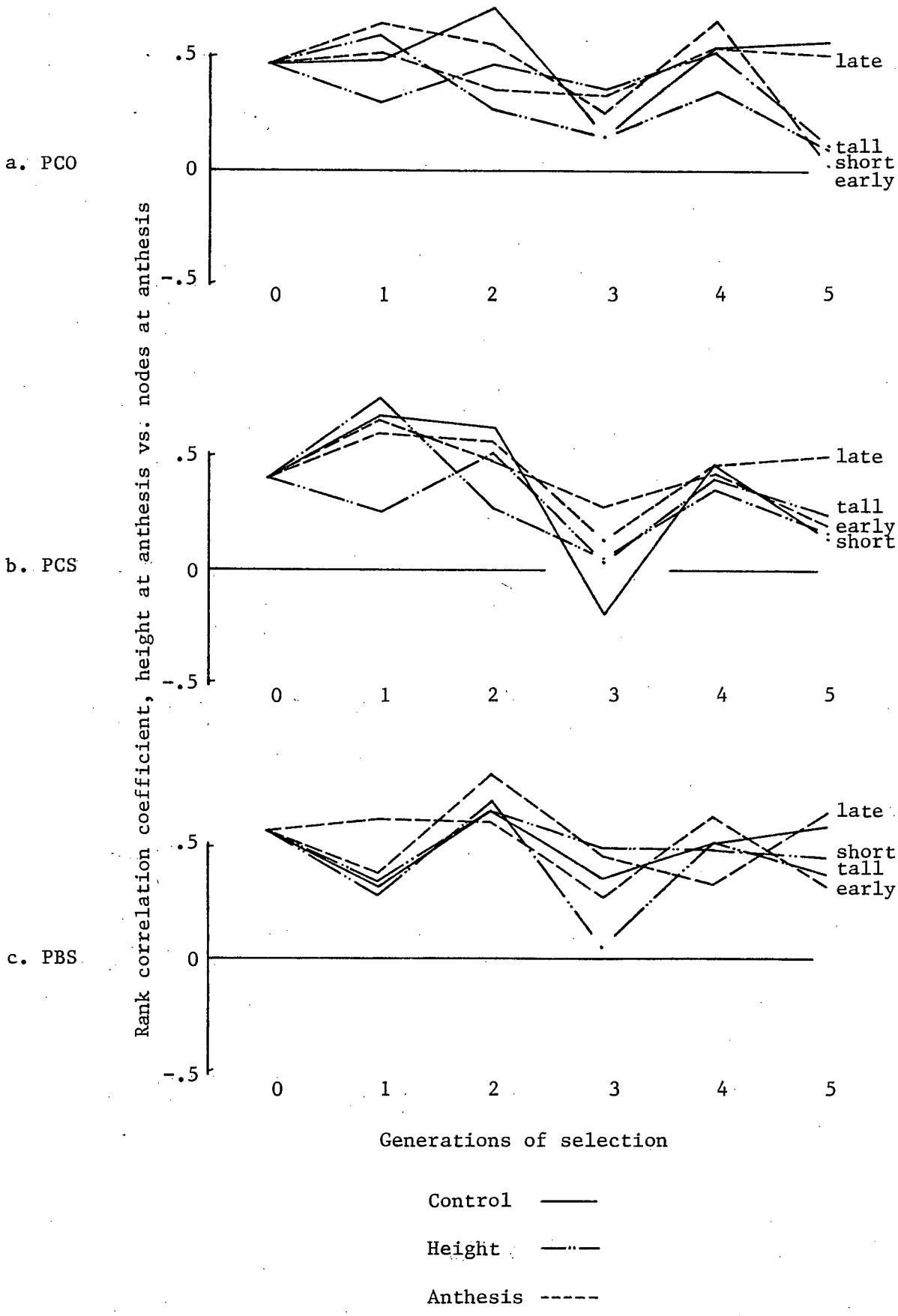
Figure 37. Correlations between height at anthesis and number of nodes at anthesis. Spearman's rank correlation coefficient is graphed for every population. Correlation coefficients which are significant at the 5% level are joined by a continuous line; lines are broken at those generations in which the correlation was not significant at the 5% level.

a. Correlations in PCO populations.

b. Correlations in PCS populations.

c. Correlations in PBS populations.

Figure 37.


a. PCO
b. PCS
c. PBS
Rank correlation coefficient, height at anthesis vs. nodes at anthesis
.5
0
-.5
0
1
2
3
4
5
late
tall
short
early
Generations of selection
Control
Height
Anthesis

Changes in qualitative characters

A number of qualitative fruit characters were recorded in the P. congesta lines, namely numbers and frequencies of winged and wingless fruited plants from generation to generation, numbers and frequencies of the various pubescence patterns, and numbers and frequencies of various fruit colours. The winged and wingless frequncies in the experimental populations are presented in Figure 11, and the frequencies of the pubescence patterns in Figures 7 to 10. I decided that the fruit colour scoring was too arbitrary and likely to have been subject to systematic change over the six generation period, and so have not attempted to include an analysis of this character. There are definitely different colour morphs in this species which, like the wing shape character are fairly constant within plants and variable between, but a more reliable and objective scoring procedure needs to be devised to work with them.

Winged and wingless plant frequencies

There is no evidence of anything other than random drift affecting the phenotype frequencies at the fruit wing locus. There is no consistent divergence or other relationship between the plus and minus selected lines, whether selected for flowering time of height at anthesis. The increase in variance in the observed frequencies among the lines (from 0 to 0.020 in the PCO lines and from 0 to 0.043 in the PCS lines) is not significantly different from the dispersion expected to result from random drift (from 0 to 0.022 in 4 generations) (Falconer, 1960).

Pubescence patterns

The situation with the pubescence patterns is similar to that with the fruit wing phenotypes. There is no apparent pattern or trend in the frequencies which might be explained by or attributed to the selection procedure. In this case the increase in variance among the PCO lines appears to be slightly larger than among the PCS lines, particularly in pubescence types 2, 3, and 4, but as the genetic mechanism controlling the character is unknown, the change in dispersion cannot be compared to any theoretical prediction, as it could in the case of the fruit wing locus. As may be expected in such relatively small, inbred populations, the rarer phenotypes 0 and 1 have been lost in many of the lines.

Aberrant characters

The frequencies of the various individuals or characters observed are presented in Table VII. The overall trend was towards an increase in frequency compared to the frequencies observed in the base populations. The PCO late and PCS short lines had particularly high frequencies of abnormal types, and the P. congesta populations produced significantly more abnormals than the P. brachystemon populations ($\chi^2_{df=1} = 67.95$, $p < 0.0001$). The G_5 source populations had low frequencies of aberrant types, similar to the frequencies observed in the G_0 base populations, to which they are comparable ($\chi^2_{df=1} = 0.85$, $p \doteq 0.4$).

Comparisons between the internal control populations and the G_5 source population.

Table VII. Frequencies of aberrant individuals.

	Cotyledons						Seedlings									Habit		
	Three			Fused			Chlorotic			Dark Pigment			Others					
	PCO	PCS	PBS	PCO	PCS	PBS	PCO	PCS	PBS	PCO	PCS	PBS	PCO	PCS	PBS	PCO	PCS	PBS
G_0	2						6	2								1	1	1
G_1	3	3		1	2		1	5		12	5	6				2	2	
G_2	3	1		1	1	2	5	7	1	12	15	2		1		10	11	11
G_3	3	3	2		2		5	4			1					6	9	1
G_4	4	4	1	1	1		9	3		2	1	1			1	15	12	3
G_5	7	9	5		2		2	26		14	3	2				8	8	10

	N				Frequency			
	PCO	PCS	PBS	Total	PCO	PCS	PBS	Total
G_0	452	453	304	1209	.020	.007	.003	.011
G_1	680	588	796	2004	.028	.029	.008	.020
G_2	806	785	765	2356	.038	.046	.021	.035
G_3	837	799	872	2508	.017	.024	.003	.014
G_4	919	858	974	2751	.034	.024	.006	.021
G_5	932	909	915	2756	.033	.053	.019	.034
G_5 source		75	93	168		.013	0	.006

The two G_5 source populations, one of P. congesta and one of P. brachystemon, were grown in order to investigate whether uncontrolled selection pressures, random drift, or other processes had affected the internal control lines.

Quantitative characters

The statistics for the measured characters in the PC source G_5 and PB source G_5 populations are presented in Table VIII, along with the statistics for the G_5 controls, for comparison.

Plectritis congesta

The P. congesta control lines did not change significantly in mean height at anthesis, number of nodes at anthesis, or number of primary branches at anthesis over the course of the experiment. There was a significant decrease in mean number of days to emergence and in days to anthesis, which may well be the result of some selective pressure for a shortened life cycle under the crowded conditions in the experimental populations. The phenotypic variance as estimated by the coefficient of variance was unchanged in all characters except the number of primary branches at anthesis, for which both control lines became significantly more variable, and flowering time, for which the PCS control line became significantly more variable.

Plectritis brachystemon

The P. brachystemon control populations developed significant

Table VIII. Measured characters: G_5 source populations compared with G_5 control populations.

	N	Mean	Standard deviation	Coefficient of variation
Days to emergence				
PCO control G_5	195	15.344	2.4198	15.77
PCS control G_5	192	15.620	2.6101	16.71
PC source G_5	74	18.554*	2.9477	15.89
PBS control G_5	187	15.829	2.7519	17.39
PB source G_5	93	17.946*	2.8028	15.62
Height at anthesis (mm)				
PCO control G_5	157	331.19	68.334	20.63
PCS control G_5	165	339.05	61.979	18.28
PC source G_5	73	315.92	53.351	16.89
PBS control G_5	153	524.42	84.939	16.20
PB source G_5	89	444.07*	55.570	12.51**
Number of nodes at anthesis				
PCO control G_5	159	7.9686	0.9963	12.50
PCS control G_5	164	8.1829	1.4197	17.35
PC source G_5	73	7.8219	1.1942	15.27
PBS control G_5	153	10.209	1.0108	9.90
PB source G_5	89	9.618*	0.9944	10.34
Number of primary branches				
PCO control G_5	158	5.5506	3.7204	67.03
PCS control G_5	165	5.5212	3.8407	69.56
PC source G_5	73	6.6301	3.5099	52.94**
PBS control G_5	153	10.993	5.0945	46.34
PB source G_5	89	11.775	7.3450	62.37**

Table VIII, continued.

	N	Mean	Standard deviation	Coefficient of variation
Days to anthesis				
PCO control G_5	163	73.736	5.1169	6.94
PCS control G_5	174	75.167	6.4217	8.54
PC source G_5	73	75.616*	4.4648	5.90** (vs. PCS)
PBS control G_5	160	93.331	4.6415	4.97
PB source G_5	91	88.835*	5.0514	5.69

* Mean values in the source populations indicated are significantly different from the control populations at the 5% level.

** Coefficients of variation in the source populations indicated are significantly different from the control populations at the 1% level.

differences from the source population over the course of the experiment for all the characters except number of primary branches. The mean number of days to emergence decreased significantly in the control line, and the mean height at anthesis, number of nodes at anthesis, and days to anthesis all increased significantly with respect to the source population.

The variance of the PBS control was significantly increased in height at anthesis, and significantly decreased in number of primary branches at anthesis; variances for the other characters were unchanged.

Correlations

There were no significant correlations in the G_5 source populations which suggested that there had been any change in the control line over the course of the experiment (Table IX).

Table IX. Correlations in the G_5 source populations.

P. congesta

Height at anthesis	-.2163			
Nodes at anthesis	-.2769*	0.1698		
Primary branches	-.3123*	0.2056*	0.3121*	
Days to anthesis	0.3443*	0.0174	0.6226*	-.0234
	Days to emergence	Height at anthesis	Nodes at anthesis	Primary branches

P. brachystemon

Height at anthesis	-.4984*			
Nodes at anthesis	-.2756*	0.2987*		
Primary branches	-.2936*	0.3381*	0.3864*	
Days to anthesis	0.1290	-.0137	0.4910*	0.0558
	Days to emergence	Height at anthesis	Nodes at anthesis	Primary branches

* Correlation coefficients significant at the 5% level.

Summary of results

Breeding system in Plectritis

Source populations

Plectritis congesta had an estimated outcrossing rate of 61.6%. In Plectritis brachystemon the outcrossing rate was not estimated, but assumed to be less than 5%.

Experimental populations

The P. congesta outcrossed populations (PCO) had an estimated outcrossing rate of 65%. The P. congesta selfed populations (PCS) had an estimated outcrossing rate of 15%. The P. brachystemon populations (PBS) had an assumed outcrossing rate of less than 5%.

Characteristics of the base populations

The mean values for days to emergence, height at anthesis, number of nodes at anthesis, number of primary branches at anthesis, days to emergence, and flowering time were greater in the P. brachystemon populations than in the P. congesta populations. P. brachystemon was more variable for days to emergence, height at anthesis and nodes at anthesis, less variable for primary branches and flowering time.

Response to selection

Selected characters

Height at anthesis

Means

The PCO lines diverged 66% or 148 mm compared to the control (+ 41%, 92mm; - 25%, 56mm); the PCS lines diverged 78% or 175 mm (+ 27%, 61 mm; - 51%, 114 mm); the PBS lines showed no divergence, but erratic fluctuations relative to the control.

Variances

There were no trends in the changes in variance as estimated by coefficients of variation; some populations showed significant increases, some significant decreases relative to the control.

Heritabilities

In PCO the realised heritability (b_c) was estimated as 0.53; heritability from parent-offspring regressions (h^2) was estimated as 0.45. In PCS $b_c = 0.58$, $h^2 = 0.44$. In PBS neither estimate was significantly different from zero.

Components of variance

Significant between family variance components were observed in most populations. There were no trends in changes in the partitioning of between / within family components over the course of the experiment.

Days to anthesis (flowering time)

Means

The PCO lines diverged 33.5% or 31.8 days compared to the control (+ 20%, 19 days; - 13.5%, 12.8 days); the PCS lines diverged 28.7% or 27.3 days (+ 16.3%, 15.5 days; - 12.4%, 11.8 days); and the PBS lines diverged 18.5% or 21.5 days (+ 12.2%, 14.2 days; - 6.3%, 7.3 days).

Variances

The trend in all six selected lines was towards a decrease in the variance of flowering time as estimated by the coefficient of variation.

Heritabilities

In PCO $b_c = 0.77$, $h^2 = 0.60$; in PCS $b_c = 0.75$, $h^2 = 0.72$;

and in PBS $b_c = 0.49$, $h^2 = 0.42$.

Components of variance

Significant between family variance components were observed in most populations. There were no trends in changes in the partitioning of between / within family components over the course of the experiment.

Unselected characters

Days to emergence

There were no strong trends in changes in means or variances. Heritability (h^2) was estimated at 0.49 in PCO control line.

Height at anthesis (in lines selected for flowering time)

There was some divergence in the means in the P. congesta plus and minus lines, but no trend in the means in the PBS lines. There were no trends in the changes in variances.

Number of nodes at anthesis

There was marked divergence in the means for all lines except PBS selected for height at anthesis. Some trend toward a decrease in variance was observed, particularly in lines selected for flowering time. Heritability (h^2) was estimated as 0.55 in PCO, 0.57 in PCS and 0.28 in PBS.

Number of primary branches at anthesis

There was some divergence in the means except for PBS selected for height at anthesis. There were erratic changes in the means from generation to generation relative to the controls. There were no trends in changes in the variances. Heritability (h^2) was estimated as 0.29 in PBS control.

Days to anthesis (in lines selected for height at anthesis)

There was marked divergence in means and a decrease in variances in the P. congesta lines; there were no trends in changes in means or variances in the PBS lines.

Fruit production

There were no trends in changes in means or variances in any of the lines.

Correlations

There were many significant correlations, both positive and negative, among the measured characters. The only significant change in correlations over the course of the experiment was the disappearance of the strong positive correlation between the two selected characters, height at anthesis and flowering time.

Qualitative characters

There was no evidence of anything other than random drift affecting the frequencies of the fruit wing phenotypes and fruit pubescence pattern phenotypes over the course of the experiment. There was some evidence of an increase of aberrant types, particularly in the P. congesta populations, which might be attributed to inbreeding.

Discussion

The questions to which this study was addressed are: 1. Is a population of inbreeding plants more or less variable genetically than a population of otherwise identical outbreeding plants with respect to quantitatively inherited characters; 2. Does the response to selection for such characters in the two populations reflect the difference; and 3. How does the genetic variability as estimated by the response to selection compare to other estimates of genetic variability in the two populations?

The experimental species

Plectritis congesta and P. brachystemon are as nearly identical as two sexually reproducing species with respectively outcrossing and selfing breeding systems are likely to be. In both vegetative habit and habitat they are nearly impossible to distinguish. They both have chromosome numbers reported of n = 16 (Morey, 1963; Taylor and Brockman, 1966). The Mill Hill populations have the required breeding system differences, with an outcrossing rate of 61.6% in the P. congesta population, and a rate of less than 5% in the P. brachystemon population.

Genetic variability and the response to selection

Direct responses

Plectritis congesta outcrossed versus P. congesta selfed

There is no evidence of any difference between the two sets of P. congesta

populations in their direct response to selection for either height at anthesis or flowering time, despite an estimated difference in outcrossing rate under the experimental conditions of about 50% (PCO t = 0.65, PCS t = 0.15). There was approximately equal change in the means, that is, a divergence of 66% in PCO, 78% in PCS plus and minus lines selected for height at anthesis, and of 33.5% in PCO 28.7% in PCS plus and minus lines selected for flowering time. There was no difference between the outcrossed and selfed P. congesta groups in the trends in the coefficients of variation, with erratic changes in both for the variability of height at anthesis, and a general decrease in both for the variability of flowering time. And, finally, the estimates of heritability were essentially the same for height at anthesis (b_c: PCO = 0.53, PCS = 0.58; h^2: PCO = 0.45, PCS = 0.44) and for flowering time (b_c: PCO = 0.77, PCS = 0.75; h^2: PCO = 0.60, PCS = 0.72). It is likely that the small population sizes in the experiment (N = 200) combined with the intensity of the selection (90%) to produce a rate of inbreeding which swamped any differences in inbreeding attributable to differences in the outcrossing rates. In comparisons with the P. brachystemon populations, therefore, I will treat the P. congesta lines essentially as duplicates, and refer to them together.

Plectritis congesta versus P. brachystemon

Height at anthesis

There was significant difference between P. congesta and P. brachystemon in response to selection for height at anthesis. The plus and minus lines diverged 66% in PCO and 78% in PCS, but no consistent divergence resulted in

the PBS lines, which fluctuated erratically. There is no difference between P. congesta and P. brachystemon in the changes in the phenotypic variance, which were erratic in all three species groups. The realised heritability estimates, however, reflected the significant response in P. congesta, which resulted in a realised heritability of 55% compared to an estimated heritability of zero for P. brachystemon, which showed no response. In effect there appeared to be no genetic variance in height at anthesis available for selection in the P. brachystemon population, but enough genetic variance present in the P. congesta populations to result in a significant response. It is interesting that while the estimated genetic variance for height at anthesis is greater in P. congesta, the phenotypic variance measured in the base populations was significantly larger in P. brachystemon. This anomaly could be explained by an increased phenotypic variability or plasticity in the genetically less variable P. brachystemon. There is a body of evidence to suggest that highly homozygous organisms may be phenotypically more variable as a result of their homozygosity, or conversely that heterozygosity has a buffering effect on phenotypic variability (Allard and Bradshaw, 1964; Baker, 1974; Bradshaw, 1965; Dobzhansky and Wallace, 1953; Falconer, 1960; Lerner, 1954; Lewontin, 1957). In a study of P. congesta, six metrical characters - height, dry weight, degree of branching, number of primary branches, number of secondary branches, and number of nodes - were all more variable in plants homozygous for either the dominant or recessive allele at the fruit wing locus, than in plants heterozygous at the same locus. Whether the plants were grown in a warm, dry environment, or in a cool, wet environment, this buffering effect of heterozygosis was apparent (Carey and Ganders, 1980; Carey, unpublished). In Limnanthes, Brown and Jain (1979) found that the selfed L. floccosa

showed more phenotypic plasticity than the outcrossed L. alba. Harding et al. (1974) found similar results working with the Lupinus nanus group of subspecies, in which the more highly selfed subspecies were more variable phenotypically than the outcrossed subspecies. Finally, Avena barbata, a more highly selfed species than its relative, A. fatua, is also more variable phenotypically, but maintains less genetic variability and responds less well to selection (Jain and Marshall, 1967, 1970).

Flowering time

The direct response to selection for flowering time also differed between the two species, but the differences were not marked, and only appeared in the fifth cycle of selection. Through the fourth cycle of selection there was no appreciable difference, with PCO, PCS, and PBS lines responding equally well to selection and diverging about 20% compared to the control (Figure 14). In the fifth cycle, the P. congesta lines continued to diverge, with a final divergence of 33.5% (PCO) and 28.7% (PCS), but the P. brachystemon populations ceased to diverge, with the final divergence being only 18.5% of the control value. The phenotypic variances (Figure 15) followed a similar pattern, with a relatively steady decrease over the first four cycles for all three species groups. The decrease continued in the fifth cycle in the case of the P. congesta, but not in the case of P. brachystemon, in which the phenotypic variance increased again. Finally, the realised heritability estimates for flowering time showed approximately equal heritability in the PCO and PCS lines (0.77 and 0.75) and slightly less, but still appreciable heritability in the PBS lines (0.49). All of the evidence indicates that there is substantial genetic variance for

flowering time in both Plectritis species, with somewhat more in P. congesta than in P. brachystemon. The fact that the response of P. brachystemon was similar to that of P. congesta for the early generations, and then changed abruptly in the fifth generation, may indicate that the genetic variance is organized differently in the selfed species. This is not unexpected; since there is so little outcrossing in P. brachystemon populations, the genetic variance in these populations could be expected to derive largely from differences between families, that is, between one or a number of relatively highly homozygous lines. The selection response would then represent selection of families rather than individuals, and the depletion of the variance and tailing off of the response would occur rapidly, particularly in small populations such as those maintained in this experiment. In contrast, P. congesta could continue to maintain genetic variance between and within families, in spite of the selection pressure, by means of the recombination coming directly from outcrossing, and from segregation in subsequent generations.

Confounding phenomena

There are a number of phenomena which could potentially confound the effects of direct selection on flowering time and height at anthesis. The first is sampling error (genetic drift), which could operate against the direction of selection in very small populations. The selective pressures used in this experiment were large enough to reduce to insignificance the possibilities that drift could affect the characters under direct selection. There is, however, evidence that random processes may have affected some of the unselected characters. The fruit wing phenotype and fruit pubescence

pattern frequencies increased in variance among the various P. congesta lines over the course of the experiment, and the increase in dispersion was not inconsistent with that expected to result from random genetic drift; certainly there seemed to be no connection between the changes in particular lines and the selection pressure.

A second factor which might have affected the response to selection is the effect of selective forces accompanying the response to the intended artificial selection, which act to counter or reduce that response. These could include, for example, reduced viability or reduced fecundity in the selected individuals or their progeny in proportion to the degree to which they depart from the control mean. There was some evidence of a decrease in viability and fecundity in some of the extreme individuals, especially those individuals which were very short and those which flowered very late in all three species groups. Since the criteria for selection included survival to produce at least ten apparently viable fruits (except in those cases noted, that is, PCS short G_3 and PBS short G_3) the effect of this counter selection was reduced somewhat. There was no obvious reduction in the total population rates of germination, survival, fitness, or fruit production in the later generations, and no notable difference between P. congesta and P. brachystemon in the deleterious effects of selection.

A third factor which might have affected the direct response to selection is inbreeding depression. In particular, this might be expected to have affected the outcrossed P. congesta. Inbreeding in the experimental populations, which was unavoidable with such small populations and heavy selection, might result in an increase in homozygosity which could produce relatively unfit homozygous recessive genotypes. In a selfing species like P. brachystemon these unfit genotypes would presumably have been selected

against and eliminated from natural populations. If the unfit homozygotes were involved in the characters being selected, their deleterious effect would be equivalent to the counter selection mentioned above, except that the same inbreeding depression would be expected to affect the control (unselected) lines more or less equally with the selected lines. There was some evidence of inbreeding effects in the increase in frequency of aberrant individuals over the course of the experiment. Plants with abnormal numbers of cotyledons or fused cotyledons, chlorotic seedlings, excessively pigmented seedlings, and plants with other abnormalities in their habit all increased in frequency, particularly in the P. congesta populations. There was no evidence that aberrant types increased in frequency in the treatment populations any more than in the control populations, though some lines had particularly high frequencies in most generations (PCO late and PCS short). The higher frequencies noted in P. congesta as compared to P. brachystemon were to be expected, since the selfed species would be less likely to retain deleterious recessive alleles in the population. The G_5 source populations had low frequencies of aberrant types, comparable to the frequencies in the G_0 populations.

Indirect responses to selection

Unselected characters

There was considerable change in the unselected characters, some of which could be attributed to selection. As mentioned above, the fruit phenotypic frequencies in the P. congesta lines seemed to change more in response to random drift than in response to selection pressure. In most

of the metrical characters, however, there were changes in the means that could be related to the selection pressure. This could be seen most often as a divergence between the plus and minus lines, with all three plus lines (PCO, PCS, and PBS) having higher mean values than the corresponding minus lines. In many cases, the divergence between the plus and minus lines was not accompanied by a divergence of both away from the control line, that is, either the plus or the minus line in these cases was not significantly different from the control, though both were significantly different from the other selected line. Thus, days to emergence measured in each of the plus lines was greater than in the minus lines by the fifth cycle of selection, except in the PBS lines selected for height at anthesis; height at anthesis in the lines selected for flowering time was greater in the plus lines than in the minus lines except in the PBS lines; in all cases the number of nodes at anthesis was greater in the plus lines than in the minus lines; number of primary branches at anthesis was greater in plus lines than in minus lines except in the PBS lines selected for height at anthesis; and flowering time in those lines selected for height at anthesis was greater in the plus lines than in the minus lines. The measurement of fruit production was subject to a large error, and I found no consistent trends which could be attributed to selection.

The fact that in general the unselected characters tended to track the selected characters is reflected in the relatively strong correlations among the characters. Thus, flowering time and number of nodes at anthesis were strongly correlated, and the coincident changes in mean values reflect this. Height at anthesis and flowering time were strongly correlated in the first three generations, which probably explains the initial divergence in flowering time observed in the plus and minus lines selected for height at

anthesis. Days to emergence and flowering time were strongly correlated, as were height at anthesis and number of nodes at anthesis. If the correlations do indicate some degree of underlying genetic linkage, then the response of the unselected characters may have been due in part either to a direct link with the selected characters which were themselves responding to selection (nodes at anthesis, height at anthesis, and days to emergence correlated with flowering time in lines selected for the latter; flowering time and number of nodes at anthesis correlated with height at anthesis in lines selected for the latter). Alternatively an indirect link through one of the unselected characters could conceivably have produced the response (days to emergence correlated with flowering time in lines selected for height at anthesis).

Other selection studies

The results I observed in this experiment are comparable to the results in such other selection experiments as were designed similarly, that is, with mass selection in a population that has not been radically altered in its genetic characteristics by inbreeding (in outcrossed taxa) or by outcrossing (in selfed taxa), and where generations are produced by a more or less natural breeding programme.

There are few reports in the literature of a lack of response to selection, largely, I suppose, because selection <u>is</u> successful to some degree in most cases. In the studies mentioned in the introduction (pp. 17 - 20), the 21 cases in outcrossed taxa for which a per cycle response was recorded had an average change in the mean value of the selected character of 14.8% per cycle of selection. In the selfing taxa, the 15 cases where a

per cycle response was recorded had an average change in the mean of 8.3% per cycle. If the two Plectritis species are treated in the same way, the average per cycle change in the mean value of the two selected characters was approximately 5% in P. congesta and approximately 1% in P. brachystemon.

Some of the selection studies reported in the literature used the same characters as I did, that is, height and flowering time, although height was not always measured at the same stage of the life cycle. In Limnanthes alba, an outcrosser, selection for height resulted in a 6% change per cycle of selection (Jain, 1979). Three studies involved selection for height in selfed taxa, with responses respectively of 4.5% per cycle in Avena sativa (Geadelmann and Frey, 1975), 12.5% per cycle in A. fatua (Imam and Allard, 1965), and 2.8% per cycle in Sorghum bicolor (Foster et al., 1980); the mean response in selfed taxa was 6.6% per cycle. Both breeding system groups had a response to selection for this character similar in degree to the response of 7.2% per cycle ($\pm$ 66% in PCO, $\pm$ 78% in PCS after 5 cycles) noted in P. congesta.

Selection for flowering time has been reported in a number of species. Among selfing taxa, in Avena sativa Geadelmann and Frey (1975) found a response to selection of 22% per cycle; Imam and Allard (1965) noted a response of 20.5% per cycle in A. fatua; and in Sorghum bicolor Foster et al. (1980) found a response of 0.6% per cycle. In Brassica campestris var. brown sarson Murty et al. (1972) observed a response of 1.7% per cycle. The mean response in these taxa is about 12% per cycle, which is considerably higher than either the 3% per cycle response in P. congesta or the 2% per cycle response in P. brachystemon. The longer the selection continues, the lower will be the per cycle response, as the total response will decrease with the depletion of genetic variance. The two experiments with Avena, in which the

per cycle response was relatively high, involved only one cycle of selection, whereas the experiments with Sorghum and Brassica involved 10 and 3 cycles respectively.

Allowing for these differences between experiments, the response to selection for the two characters, height and flowering time, in both Plectritis species would seem to fall well within the range of observed responses in other plant species.

To answer the first two questions posed at the beginning of the discussion, the Plectritis brachystemon population, which is highly inbred, has significantly less genetic variability for one quantitatively inherited character, height at anthesis, than the P. congesta population, which is highly outbred but otherwise nearly identical; the difference between the two species in levels of genetic variability is reflected in the response to selection for height. In contrast, however, there is considerable genetic variability for the second quantitatively inherited character, flowering time, in both populations, and this, too, is reflected in the response to selection for this character. The levels of genetic variability and selection response for both characters in Plectritis are similar to those found in other plant species.

The third question was how independent estimates of genetic variability compare to the estimates derived from the response to selection for the two quantitative characters.

Independent estimates of genetic variability in Plectritis

There is ample evidence (based mainly on isozyme data) to indicate

that outcrossed taxa are more diverse, that is, more highly heterozygous and more polymorphic on average, than are selfed taxa. The evidence from the studies of Layton (1980) in P. congesta and P. brachystemon is in agreement with this. He calculated Nei's index of gene diversity within populations for the two species to be 0.22 for P. congesta and 0.06 for P. brachystemon. Ganders and Maze (unpublished) studied fruit wing characters measured in two populations of P. congesta and one of P. brachystemon and concluded that the variability in the outcrossed species was significantly greater than that in the selfed species.

The two particular populations chosen as sources for this experiment differ in the amount of phenotypic variability shown in certain characters. The P. congesta population at Mill Hill is polymorphic for a number of fruit characters: presence or absence of fruit wings, pubescence pattern, wing shape, and fruit colour. The P. brachystemon population, in contrast, is monomorphic: all plants produce medium brown wingless fruits with the same pubescence pattern.

The base populations, G_0, which are presumed to be a random or unselected sample of genotypes in the source populations, also provide some evidence of differences in variability. For the measured characters the coefficients of variation were significantly different between the two species in 5 of 6 cases, with the coefficient being larger in P. congesta for the number of primary branches at anthesis and flowering time, and larger in P. brachystemon for number of days to emergence, height at anthesis, and number of nodes at anthesis. These coefficients are based on variances which are essentially phenotypic, although the environmental component has been reduced by the use of a common controlled environment. It is possible that the greater variability shown by P. brachystemon for three characters is due

to phenotypic plasticity, about which I will say more later. The final evidence, independent of the selection experiment, for differences between the two species in variability comes from the estimates of heritability from the parent-offspring regressions in the three control lines. For the two selected characters (Table V) P. brachystemon has considerably less genetic variance as estimated by heritability for height at anthesis (essentially none as compared to 45% for P. congesta), and only slightly less genetic variance for flowering time (42% as compared to 60-70% for P. congesta). For the unselected characters (Table VI) there are too few good estimates of heritability to make a comparison between P. congesta and P. brachystemon possible, except in the case of the number of nodes at anthesis. In this case the heritabilities are comparable to those estimated for flowering time, with P. brachystemon showing less genetic variance (h^2 = 0.28) than P. congesta (h^2 = 0.55), but both species having low to intermediate heritabilities for the character. The similarities in the heritabilities for these two characters, flowering time and number of nodes at anthesis, is not surprising considering the strong and consistent positive correlation between them, which was evident in all experimental populations (Figure 35). It is interesting that the coefficient of variation for number of nodes at anthesis was greater in P. brachystemon G_0 than in the two P. congesta G_0 populations, while the heritability estimates indicate that genetic variance is greater in P. congesta. There are similar anomalies which were noted when comparing the results of the selection experiment with the G_0 coefficients of variation, and they will be discussed in the following sections.

The answer to the third question posed at the beginning of the discussion, then, is that the independent evidence of genetic variability in the two

species is equivocal. Most of the characters are more variable in the outcrossed P. congesta than in the selfed P. brachystemon. These include the isozyme and fruit phenotype polymorphisms, and the phenotypic variances in number of primary branches and flowering time in the base populations grown in controlled and identical environments. These characters agree with the levels of variability in height at anthesis as observed in the response to selection. The phenotypic variances of days to emergence, height at anthesis, and number of nodes at anthesis in the G_0 populations are higher in the P. brachystemon populations than in the P. congesta populations. If we assume that the environmental components are constant in both species (perhaps a tenuous assumption) then this evidence would indicate that there was more genetic variability in the selfer than in the outcrosser. None of the independent evidence agrees closely with the observed levels of approximately equal genetic variance in both species in response to selection for flowering time.

The effects of breeding system on the population genetic structure of Plectritis

The two species of Plectritis are very similar in habit and habitat, but are well distinguished by their breeding biology and population genetic structure. Isozyme studies show that the genetic diversity is much greater in total and within populations in P. congesta than in P. brachystemon; most of the genetic diversity in P. brachystemon is between populations (Layton, 1980). Similarly, the genetic diversity in the fruit phenotypic characters - presence of fruit wings (for which the genetics are known), pubescence pattern, wing shape, and fruit colour (for which the genetics are

not known) - is greater in P. congesta populations than in P. brachystemon populations. With respect to the fruit phenotype characters, the Mill Hill populations of Plectritis are typical, that is, P. congesta is relatively highly polymorphic and P. brachystemon is monomorphic. The isozyme patterns in these particular populations have not yet been studied.

A largely winged-fruited population of P. brachystemon was less variable for fruit wing characters than two comparable winged populations of P. congesta; this comparison dealt with the phenotypic variability of the characters that were measured, but the particular characters are certain to have a small or negligible environmental component (Ganders and Maze, unpublished).

The phenotypic variability of the two Mill Hill populations as estimated by the variances in the G_0 populations was greater for P. brachystemon in some cases and for P. congesta in others. In the cases where the genotypic component of this variance could be estimated, either by parent-offspring regressions or by the response to selection, P. congesta was the more variable taxon genetically, although significant genetic variance was indicated for P. brachystemon in number of nodes at anthesis and flowering time. In two cases, height at anthesis and number of nodes at anthesis, P. brachystemon was more variable phenotypically but less variable genetically than P. congesta, a result which can only be explained by postulating a relatively higher element of phenotypic plasticity in P. brachystemon, at least under the experimental conditions.

Plectritis brachystemon

Plectritis brachystemon, a highly selfed species, appears to have lost

genetic diversity as a consequence of having evolved a selfing breeding system. It has not lost all of its genetic variability for some characters, however, and there presumably has been some selection pressure to maintain genetic variance in flowering time and number of nodes at anthesis, while genetic variance for height at anthesis has been lost. The difference between the low genetic diversity as estimated from isozymes and fruit characters, and the presence of significant genetic variance in other characters can be explained in a number of ways. Occasional outcrossing events which occur in habitually selfing populations will continue to segregate heterozygous individuals for a number of generations, subject to the forces of random drift, inbreeding, and selection. In this case the low genetic diversity in the isozymes and low genetic variance in height at anthesis could be the result of selection acting on these characters, reducing their variability. Conversely, the high genetic variance in flowering time and number of nodes could represent the level of variability maintained by occasional outcrossing and segregation. This explanation requires that the genetic determinants of flowering time and number of nodes be nearly neutral, and that the outcrossing rate be high enough and population sizes large enough to permit accumulation of these heterozygous types. None of these assumptions is reasonable for P. brachystemon populations.

Alternatively, the low genetic diversity in isozymes and low genetic variance in height at anthesis could be mainly the result of the high levels of inbreeding, small population size, and random loss of alleles. The relatively high genetic variance in flowering time and number of nodes could be the result of selection for variability. The balance of selective and random forces acting on isozymes is still a subject of much debate, but there

is probably selection acting on at least some of the loci, and there is likely to be selection affecting height at anthesis to some degree in natural populations. It is likely that the actual situation in P. brachystemon populations is somewhere between the two extremes. There is probably some selection acting on isozymes and height, but the low levels of genetic variability in these traits relative to P. congesta reflect largely the effects of breeding system and random loss of variability. The relatively high genetic variance in flowering time and nodes at anthesis is probably maintained by selection.

Selective forces which maintain variability involve a number of mechanisms. Those which involve mutation, migration, or disassortative mating as sources of new variability are not likely to be the major forces involved in the short term in P. brachystemon populations. A form of selection which is more plausible in this light is heterozygote advantage. Heterozygote advantage can be used in a narrow sense, referring to an absolute fitness advantage of a heterozygote over homozygotes under all conditions, or in a broad sense, where the net fitness advantage of the heterozygote only appears as the fitness values of the various genotypes change in time or space. Heterozygote advantage has been demonstrated to operate in P. congesta under some conditions at the fruit wing locus (Carey and Ganders, 1980) and may be a factor in preserving some of the polymorphism in that species. In P. brachystemon, however, there are probably too few heterozygotes produced in natural populations to permit heterozygote advantage to be a factor in the maintenance of genetic variance. The frequency of heterozygotes at the fruit wing locus in one population was estimated to be less than 3% (Ganders et al., 1977b); the frequency of heterozygotes observed at polymorphic isozyme loci in P. brachystemon

populations averaged 0.45% (Layton, 1980). There is some evidence that heterozygote advantage may be operating in some selfing species to maintain variance (Allard, Jain and Workman, 1968; Jain and Allard, 1960). All of this evidence comes from characters in which the genotypes can be observed (monogenic or simply inherited characters). Maintenance of genetic variance in quantitatively inherited characters by heterozygote advantage in a selfing species requires even higher rates of production of the heterozygotes than those required to maintain monogenic polymorphisms. The most likely form of selection to maintain genetic variability in P. brachystemon populations is some type of patterning of the selective pressures either in time or in space. If microhabitats and their associated selection pressures occur patchily or form a mosaic, then the segregating lines which result from the rare outcrossing events in P. brachystemon populations could be maintained, highly homozygous within each microhabitat but with different genotypes in different microhabitats. That genetic variance is divided among a number of homozygous lines in P. brachystemon is also suggested by the observed form of the response to selection for flowering time. A relatively large response in the early generations, followed by a rapid tailing off in the last generation, could occur as the selected lines were reduced in number and variance between the lines was no longer available for selection. It is possible that an examination of a number of the isozyme loci simultaneously in individuals from P. brachystemon populations would reveal a number of lines of different multilocus homozygotes; the levels of isozyme polymorphism discovered to date in populations would allow for a maximum of 11 different homozygous lines per population at 13 isozyme loci (Layton, 1980). The isozyme data in Plectritis have not been analysed in this way to determine multilocus genotypes, but there is evidence from other

predominantly selfing species for a population structure composed of lines of homozygous genotypes. In Avena barbata a number of studies have indicated that in some populations a few multilocus genotypes are present in excess over the expected frequency, and appear to be adapted to different microhabitats within the habitat (Allard et al., 1972; Clegg and Allard, 1972). Multilocus organization in A. fatua and Festuca microstachys populations has also been studied and a similar situation noted (Allard, 1975).

The question that follows logically from the observation of genetic variability in P. brachystemon is why there might be such relatively strong selection to maintain variability in flowering time and number of nodes at anthesis in the species, to the point that it is nearly as variable as P. congesta. Since P. brachystemon is highly self-pollinated, there is not likely to be a connection with pollinator behaviour as might be the case in the outcrossed species. In P. congesta, variability in flowering time (and number of nodes, which are correlated) could serve to extend the flowering period in the population, thus decreasing the chance of poor fruit set due to lack of synchrony with the activity of particular pollinators. This is particularly likely in a species like P. congesta which does not appear to rely on one major pollinator, but rather a number of pollinators.

One possible explanation for the advantage to be gained from variability in flowering time in P. brachystemon is that it reflects variability in some physiological or developmental character which is subject to multiniche selection. Alternatively, flowering time may be directly subject to such disruptive selection. For example, it is possible that in microsites which dry early in the season, early flowering is selectively advantageous, while in wetter microsites, delaying flowering may maximize fecundity.

In contrast to the genetic variability present in flowering time are the relatively higher levels of phenotypic variability for height at anthesis observed in P. brachystemon, compared to those in P. congesta. This plasticity may be advantageous in populations exposed to a mosaic of selective forces, or it may merely be a non-adaptive side effect of the increased homozygosity which has accompanied the evolution of a highly selfed breeding system. If homozygous genotypes are by nature more plastic, there may have been no way for P. brachystemon to avoid the increased plasticity were it to have proved disadvantageous.

Phenotypic plasticity could be adaptive in a number of ways. It could make phenotypically uniform a population of plants which are genetically diverse, maintaining genetic variability in the face of stabilizing selection. Bradshaw (1965) has likened this to the effects of dominance and gives examples in which it may be operating, namely in Plantago maritima (Gregor,1956) and a number of species examined by Turesson (1922, 1925). Alternatively, phenotypic plasticity could allow phenotypic variability in a population of plants which are genotypically relatively uniform. This is the potential which has been attributed to some hypothetical weedy or colonizing species, which would be composed of one or more general-purpose genotypes, at once highly homozygous and highly plastic (Baker, 1974). There are weedy species which do exhibit more phenotypic variability in some characters than their non-weedy relatives. Examples are Sonchus oleraceus (weedy) versus S. arvensis (Lewin, 1948) and Chenopodium album (weedy) versus C. rubrum (Cumming, 1959). Similarly there are other species pairs in which the more genetically variable species is less phenotypically variable (species of Limnanthes, Lupinus, and Avena mentioned on pages 138 and 139). It is unfortunate that there are no measurements of phenotypic variance yet

available for natural populations of P. congesta and P. brachystemon, so it is not possible to compare levels of variability under natural and uniform (growth chamber) conditions, nor to estimate the extent of phenotypic plasticity in nature. The relatively large differentiation between populations of P. brachystemon in isozyme patterns (Layton, 1980), the presence of significant genetic variance in some characters, and the fact that neither P. congesta nor P. brachystemon is particularly aggressive or weedy, suggest that the notion of a species composed of general-purpose, highly homozygous, highly plastic genotypes which has been suggested for some selfing species is not an adequate description of the situation in P. brachystemon.

Occasional outcrossing and multiniche selection among the segregating lines for the genetic determinants of flowering time are likely to have been important adaptive processes in P. brachystemon. It is not possible at the moment to say whether the increased phenotypic variability in height at anthesis in P. brachystemon is or is not adaptive, or whether low genetic variability and high phenotypic variability for height in P. brachystemon and high genetic variability and low phenotypic variability for height in P. congesta are different solutions to the same evolutionary problem.

Plectritis congesta

The presence of genetic variability in flowering time, height at anthesis, and number of nodes at anthesis in P. congesta is easy to account for as a consequence of the processes of recombination and segregation accompanying the habitual outcrossing in the species. It is impossible to say whether the levels of variability so maintained are more or less than

expected. Since the habitats are similar, presumably the same type of multiniche selective pressures postulated to be operating in P. brachystemon would also affect P. congesta. Populations of the latter, however, would not be able to develop genetically differentiated local subdividions as easily, because of the mixing effect of outcrossing. In addition, unlike P. brachystemon, P. congesta has a pollination biology which could theoretically support selection for greater variability in flowering time in response to pollinator behaviour, to increase the reliability of fruit set; the origin and maintenance of genetic variability in flowering time is easily explained in P. congesta. Heterozygote advantage has been shown to operate to maintain at least one of the polymorphisms in P. congesta populations, and inbreeding depression was more marked in the experimental P. congesta populations than in the P. brachystemon populations. Given no evidence to the contrary, one may conclude that the higher levels of genetic variability and the outcrossed breeding system which generates them are both selectively advantageous for P. congesta.

Further study in Plectritis

The differences between the two Plectritis species in breeding system have definitely affected the genetic structure of their populations, inbreeding in P. brachystemon having decreased the genetic diversity of isozyme and fruit morph characters and the genetic variance in height. Yet it is obvious from the genetic variance in flowering time and the phenotypic variance in height and number of nodes that P. brachystemon has not sacrificed all of its sources of variability to its breeding system.

More study of both species is warranted, to clarify the differences and to answer what may be the fundamental evolutionary and systematic question, namely, how and why P. brachystemon evolved a selfing breeding system at some point in the past, and how and why both species are equally successful in sympatry at present.

Experiments with P. brachystemon could be designed to determine whether this taxon does in fact have a population genetic structure affected by a number of different microhabitats and multiniche selection. First, multilocus isozyme genotypes could easily be determined for a population. Since 13 isozyme loci have already been studied, and expansion of the number of loci available for characterization is quite feasible (Layton, personal communication), one should be able to differentiate a number of multilocus genotypes, if present, even within a relatively invariable P. brachystemon population. If microhabitat patterning is a factor in a population, it might be possible to detect at least some of its dimensions with suitable measurements of physical factors (soil, moisture, micro-topography) and biotic factors (correlated plant species), and relate the multilocus isozyme patterns to particular microhabitats, as has been done with other species (Allard et al., 1972; Allard, 1975). Since comparisons with sympatric P. congesta populations are possible, one could do the same thing with that species, to verify whether the effect of oucrossing has been to produce the expected larger number of isozyme genotypes, but without any subdivided pattern based on microhabitat differences.

One of the most interesting experiments would involve measurements of the phenotypic variance in natural populations of both species for the characters used in this experiment, in order to estimate the naturally occurring levels of phenotypic plasticity. For example, under experimental

conditions P. congesta was genetically more variable for height than was P. brachystemon, but phenotypically less variable. One could measure the phenotypic variance for height in natural populations to see if the different levels of genetic variability translate into similar or dissimilar levels of phenotypic variability under natural conditions.

As a final example, one could extend the studies to other species in the genus, which because of their floral morphology are presumed to be more highly selfed than P. congesta, and to other sections of the ranges of P. congesta and P. brachystemon. There are reports of populations of the two species in the more southerly parts of their ranges which are more similar to each other than are any that have been studied in British Columbia (Morey, 1962). This appears to be the case in some populations observed recently in California, and it would be interesting to see how extensive the apparent intermediacy is, in terms of breeding system and population genetics and biology. Jain et al. (1970) have pointed out the danger in extending arguments from studies of a population in one area to other species or other populations in the same species; populations of P. congesta in the southern part of the range appear to be far less polymorphic within populations for some fruit characters than are those in British Columbia.

Implications for other studies

The estimation and comparison of levels and organization of genetic variability in relation to breeding systems in various organisms is an active area of study among population geneticists. In this field it is important to distinguish between potential or hidden genetic variability

(genetic diversity) and realised or free genetic variability (genetic variance). In the two Plectritis species studied here, a reasonably good relationship was observed between the breeding system, the amount of genetic diversity, and the level of genetic variance present in a population. In comparison to the outcrossed P. congesta, the selfed P. brachystemon has less genetic diversity and less genetic variance. There is, however, still considerable genetic variance in the P. brachystemon for at least one character, flowering time, perhaps more than one would expect from such a highly selfed organism, or on the basis of the lack of diversity in the isozymes. Moreover, the levels of phenotypic variability measured in some of the characters indicate more variability in P. brachystemon than in P. congesta; this may be misleading, however, as in at least one case (height at anthesis) the difference is caused by high phenotypic plasticity rather than genetic variability.

In studies where isozymes are being examined, it is important that a lack of genetic diversity in isozymes not be interpreted to indicate a general lack of genetic variance in all characters, without other supporting evidence. Isozymes have so far proved to be good indicators of relative levels of variability, for instance between outcrossers and selfers in general; nevertheless, amounts of genetic variance which are significant from an evolutionary point of view can be maintained along with isozyme monomorphism. Isozymes will and should continue to be used to estimate population genetic parameters because they are more nearly estimates of the genotype than are characters which have a large environmental component to their variation. Allele frequencies at many individual loci can be examined, and the sampling is relatively fast, easy, and precise. Their contribution to the phenotype, other than their electrophoretic mobility,

is often unknown, and their selective values are correspondingly difficult to interpret.

When studies are directed to variability of quantitative characters in populations, the roles of genetic variance and phenotypic plasticity or environmental variance should be assessed carefully. Lacking evidence as to the genetic components of variance, it may be tempting to argue that an outcrossed population which is phenotypically more variable than a selfed population is expressing higher levels of genetic variance. By the same reasoning, a selfed population that is more variable than an outcrossed one might be regarded as exhibiting characteristically higher levels of phenotypic plasticity. Some of the earlier descriptions of increased phenotypic plasticity in weedy or selfing plant species have been based on observations of phenotypic variance in comparison with related non-weedy or outcrossing species, and are not accompanied by an estimate of the genetic component of the variance (for example Cumming, 1959 and Lewin, 1948). Later studies, such as those with Lupinus (Harding et al., 1974), Limnanthes (Brown and Jain, 1979),and Avena (Jain and Marshall, 1970), have estimated the genetic components; difficult as they may be to obtain, such estimates do a great deal to increase our confidence in speculations about the contribution of genetic variance vs. phenotypic plasticity in strategies of populations of various species.

Selection experiments may not be the fastest way to study the genetic components of variation in quantitatively inherited characters. It may be faster to do large scale breeding experiments of the type which are common in crop science and agricultural research (various controlled crossing methods and progeny testing methods). Selection experiments have the advantage of smaller space requirements, and consequently better control

of the environmental heterogeneity may be possible. Estimates of genetic variance in quantitative characters are an invaluable addition to electrophoretic studies, if the population genetics or biology of a plant are to be fully understood. They reflect a different and in some ways more biologically meaningful portion of the phenotype than do isozymes.

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Between family / within family variance ratios in experimental populations.

a. PCO populations.

Treatment	Generation	Days to emergence	Height at anthesis	Nodes at anthesis	Primary branches	Days to anthesis	Fruit production
Control	G_1	1.02*	1.82	2.30	1.31*	2.15	1.40*
	G_2	3.13	10.82	5.13	4.16	8.52	2.93
	G_3	3.82	5.71	3.21	1.28*	6.63	1.53*
	G_4	3.11	9.44	3.91	3.82	6.36	2.39
	G_5	6.34	3.85	1.93	1.89	2.54	
Early anthesis	G_1	1.54*	2.53	2.99	1.87	1.40*	1.01*
	G_2	2.43	7.05	3.74	7.44	2.74	2.34
	G_3	5.82	2.60	4.68	1.63*	1.86	2.22
	G_4	2.89	6.61	3.71	3.52	3.11	1.79
	G_5	2.99	6.63	4.49	3.15	2.38	
Late anthesis	G_1	1.40*	4.58	2.23	1.75	2.07	1.24*
	G_2	1.91	3.43	4.01	1.37*	3.11	1.74
	G_3	2.35	8.14	2.56	2.73	2.51	1.12*
	G_4	4.00	3.36	4.76	2.14	3.95	3.45
	G_5	3.22	5.30	3.75	3.18	3.35	
Short height	G_1	2.66	3.49	2.90	2.56	6.44	7.30
	G_2	1.98	2.66	3.11	2.31	4.72	2.25
	G_3	1.03*	2.87	5.31	3.20	4.54	2.37
	G_4	1.79	4.09	5.22	1.58*	4.41	1.54*
	G_5	3.61	5.43	4.83	7.84	4.47	
Tall height	G_1	4.25	1.06*	2.26	2.75	1.59*	1.04*
	G_2	3.40	4.72	1.87	2.28	2.97	2.38
	G_3	6.04	3.33	3.58	0.75*	2.69	1.40*
	G_4	2.91	4.17	6.14	2.73	5.15	1.57*
	G_5	2.86	1.80	5.86	3.60	2.95	

b. PCS populations.

Treatment	Generation	Days to emergence	Height at anthesis	Nodes at anthesis	Primary branches	Days to anthesis	Fruit production
Control	G_1	1.68 *	4.99	2.93	1.73	3.36	0.86 *
	G_1^2	2.92	6.03	9.97	3.09	9.76	2.40
	G_2^3	6.16	3.07	6.61	1.70	6.96	1.85
	G_3^4	3.75	5.99	11.95	6.66	11.53	1.57 *
	G_4^5	3.17	5.37	6.92	2.73	6.09	
Early anthesis	G_1	1.77	2.28	2.59	1.95	2.84	1.44 *
	G_1^2	2.20	5.07	4.00	6.78	5.34	3.91
	G_2^3	9.78	3.71	3.35	3.38	4.64	2.15
	G_3^4	1.65 *	1.34 *	3.94	2.73	4.05	1.91
	G_4^5	3.02	7.01	6.58	1.94	6.73	
Late anthesis	G_1	1.51 *	4.41	3.39	1.17 *	2.59	1.17 *
	G_1^2	3.62	5.40	4.50	1.65 *	1.87	2.48
	G_2^3	5.27	2.91	5.24	6.99	2.13	1.24 *
	G_3^4	2.60	6.96	4.45	2.74	2.51	3.48
	G_4^5	2.00	5.14	6.43	4.22	3.66	
Short height	G_1	2.52	1.57	7.50	4.63	6.20	1.23 *
	G_1^2	2.04	2.67	6.06	2.74	4.97	4.59
	G_2^3	3.96	5.39	8.40	6.44	8.88	2.26
	G_3^4	—	—	—	—	—	—
	G_4^5	1.60 *	5.83	15.09	4.24	6.59	
Tall height	G_1	1.17 *	3.41	3.74	2.48	6.88	3.72
	G_1^2	1.17 *	3.06	5.53	2.54	5.40	3.47
	G_2^3	2.42	3.83	10.71	2.44	4.80	1.13 *
	G_3^4	1.87	7.53	6.24	4.63	4.35	2.06
	G_4^5	1.63 *	4.22	4.00	2.12	4.40	

c. PBS populations.

Treatment	Generation	Days to emergence	Height at anthesis	Nodes at anthesis	Primary branches	Days to anthesis	Fruit production
Control	G_1	2.15	4.66	3.23	4.19	4.47	1.36*
	G_2	2.34	21.49	5.18	10.69	3.57	3.29
	G_3	3.09	5.13	3.64	4.83	6.53	2.19
	G_4	2.27	2.81	3.18	4.76	5.60	3.03
	G_5	1.33*	2.42	1.88	2.59	1.39*	
Early anthesis	G_1	0.71*	1.19	2.81	1.36*	2.58	0.70*
	G_2	4.03	5.93	2.98	2.84	6.07	2.85
	G_3	1.67	2.55	2.15	1.92	2.04	1.94
	G_4	3.95	13.17	3.08	3.69	3.67	4.86
	G_5	1.59*	1.95*	1.90*	3.43	1.44*	
Late anthesis	G_1	1.32*	7.91	1.84	8.63	3.19	3.39
	G_2	1.90	4.41	2.17	1.34*	1.31*	2.06
	G_3	4.00	3.92	2.12	6.01	3.71	2.08
	G_4	1.68	2.88	2.60	1.95	3.27	4.46
	G_5	1.59*	2.09	1.36*	1.71*	4.82	
Short height	G_1	2.60	1.86	5.16	4.63	5.08	2.53
	G_2	5.33	16.20	4.37	10.36	5.72	4.96
	G_3	4.57	1.57*	5.06	2.30	3.66	1.12*
	G_4	—	—	—	—	—	—
	G_5	2.79	1.39*	1.68	1.02*	1.91	
Tall height	G_1	2.47	4.59	4.31	4.72	5.57	3.97
	G_2	1.78	8.66	2.78	5.04	1.20*	1.92
	G_3	1.54*	1.47*	4.30	2.16	2.80	1.38*
	G_4	2.86	5.85	8.57	3.58	10.22	3.02
	G_5	2.28	3.49	1.63*	2.88	10.57	

Coefficients of variation, unselected characters.

	PCO				PCS				PBS			
	Early	Late	Short	Tall	Early	Late	Short	Tall	Early	Late	Short	Tall
Days to emergence												
G_0 (Control)	22.7				22.7				27.17			
G_1	18.09	20.29	17.63	22.18	26.05	21.3	18.58	17.46	37.95	32.32	24.04	19.42
G_2	32.47	42.03	35.36	31.79	30.89	30.11	35.78	32.73	17.64	20.58	37.59	39.42
G_3	18.85	26.09	35.10	25.66	21.62	28.01	27.43	24.90	29.82	28.07	26.31	28.21
G_4	24.38	27.48	24.86	23.32	24.4	16.98	39.76	22.38	35.73	37.95	39.76	32.36
G_5												
Height at anthesis												
G_0 (Control)	20.16				20.16				23.97			
G_1	17.31	18.13			17.39	18.46			138.76	28.15		
G_2	16.53	17.62			22.23	25.13			21.81	29.62		
G_3	14.05	20.54			15.41	20.95			19.5	22.2		
G_4	17.29	16.53			17.52	21.57			30.11	19.9		
G_5												

	PCO				PCS				PBS			
	Early	Late	Short	Tall	Early	Late	Short	Tall	Early	Late	Short	Tall
Nodes at anthesis												
G_0 (Control)	12.43				12.43				14.03			
G_1	15.35	14.72	12.17	14.04	11.11	10.56	12.28	9.13	24.23	14.42	15.98	16.76
G_2	10.06	10.99	9.17	9.46	11.8	11.28	10.01	14.02	11.57	14.38	11.11	11.7
G_3	12.13	10.79	11.57	12.5	9.67	11.22	12.97	13.8	10.88	12.24	14.46	12.82
G_4	13.53	12.16	11.62	10.54	8.46	8.61	17.21	9.13	12.63	18.35	17.21	16.15
G_5												
Primary branches at anthesis												
G_0 (Control)	126.09				126.09				106.4			
G_1	251.55	125.74	566.1	177.87	233.52	136.71	4,280	173.59	33,942	154.37	240.96	237.8
G_2	118.79	89.73	123.97	126.43	111.11	112.52	138.38	102.93	111.13	102.77	95.84	84.72
G_3	——	175.47	202.05	226.35	139.12	150.31	226.35	120.09	101.58	70.11	——	98.71
G_4	172.0	235.51	208.96	143.4	81.57	97.85	160.69	157.65	571.99	308.03	160.69	180.18
G_5												

Appendix 2, continued.

	PCO			PCS				PBS			
	Early	Late	Short	Tall	Early	Late	Short	Tall	Early	Late	Short	Tall
Days to anthesis												
G_0 (Control)	7.76				7.76				6.93			
G_1			7.44	6.09			7.96	7.32			6.98	7.58
G_2			5.10	5.79			6.51	7.48			8.05	6.33
G_3			6.12	6.5			7.11	6.54			6.79	5.67
G_4			5.66	5.87			5.52	5.29			5.52	7.13
G_5												
Fruit production												
G_0 (Control)	74.99				74.99				68.8			
G_1	84.87	81.22	82.61	86.94	160.91	298.92	303.94	437.98	52.75	46.7	51.51	51.01
G_2	59.19	86.62	58.93	63.25	67.7	83.95	76.76	71.22	54.85	46.23	53.1	45.31
G_3	53.45	64.47	74.77	68.3	58.89	99.95	91.56	90.45	64.5	60.45	67.32	79.38
G_4	72.45	68.77	76.33	66.4	70.48	82.49	99.31	88.41	33.99	36.38	41.96	37.72
G_5												