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ENVIRONMENTAL, PHYSIOLOGICAL AND GENETIC INFLUENCES ON YIELD COMPONENT INTERACTIONS AND BIOMASS PARTITIONING IN WILD POPULATIONS OF HIGHBUSH AND LOWBUSH BLUEBERRIES

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ENVIRONMENTAL, PHYSIOLOGICAL AND GENETIC INFLUENCES ON YIELD COMPONENT INTERACTIONS AND BIOMASS PARTITIONING IN WILD POPULATIONS OF HIGHBUSH AND LOWBUSH BLUEBERRIES

By

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ABSTRACT

ENVIRONMENTAL, PHYSIOLOGICAL AND GENETIC INFLUENCES ON YIELD COMPONENT INTERACTIONS AND BIOMASS PARTITIONING IN WILD POPULATIONS OF HIGHBUSH AND LOWBUSH BLUEBERRIES

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The narrow germplasm base of the cultivated highbush blueberry has resulted in limited adaptability, low genetic variation and a yield plateau. Incorporation of wild, adapted germplasm into the cultivated genepool would alleviate problems associated with a restricted genetic base; however, wild material has not been examined in a systematic manner. The purpose of this study was to quantify environmental, physiological and genetic influences on growth and reproduction in native populations of highbush and lowbush blueberries. Highbush blueberry plants were found to be less efficient at producing fruit as the age of canes increased. This suggests that removing older canes by regular pruning would improve bush vigor and yield potential. Compensation was observed between inflorescence bud number/cane and berry size, but generally yield components behaved independently. A similar pattern was observed in the lowbush blueberry. Independence among components may be the result of sequential component development and independent regulation by different environmental factors. Component independence is an important characteristic and may be selectively maintained in plants encountering unpredictable environmental variation. Genotypes from shaded, dry sites exhibited greater reproduction than

those from open, wet sites. The results of this study suggest that yield potential in cultivated highbush blueberries can be improved through a variety of cultural and genetic manipulations.

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LIST OF SYMBOLS AND ABBREVIATIONS

α - level of statistical significance

β - vector of standardized regression coefficients

σ^2 - variance

AT - Adam's Trail lowbush site near Grand Marais

BG - Long Lake Bog lowbush site near Traverse City

BL - Beaver Lake lowbush site near Grand Marais

BPS - annual biomass production per individual

BR - Blueberry Ridge lowbush site near Marquette

C - factor coefficient

^oC - degrees centigrade

CA - ppm calcium

CD - Closed, dry lowbush site near Fife Lake

cm - centimeters

CO_2 - carbon dioxide

C.V. - coefficient of variation

CW - Closed, wet site near Lake City

DEN - density

d.f. - degrees of freedom

DV - Dansville highbush site

DW - distance from water

EMS - estimated mean square

F - statistical distribution for judging variance components

g - grams

GL - Gun Lake highbush site near Hastings

GM - Grand Marais lowbush site

I - identity matrix

k - bias factor used in ridge regression

K - ppm potassium

kg - kilogram

L - factor loading

LAT - latitude

LONG - longitude

LS - Lake Superior lowbush site near Grand Marais

m - meter

MB - Miner's Beach lowbush site near Munising

MD - Moderately dry lowbush site near Lake City

MG - ppm magnesium

MJ - percent soil moisture in June

MS - mean square

MW - Moderately wet lowbush site near Lake City

N - ppm nitrate

NK - North Kibbins lowbush site near Hastings

n.s. - not statistically significant

OD - Open, wet lowbush site near Traverse City

p - probability of no significant difference

P - ppm phosphorus

P - path coefficient

PAR - photosynthetically active radiation

PC - principal component

PFL - percent of a population flowering

PH - negative log of the hydrogen ion concentration

PLT - percent of ambient PAR

PN - propagule number

PORG - percent organics

ppm - parts per million

PS - propagule size

r - correlation coefficient

R^2 - coefficient of multiple determination

SK - South Kibbins lowbush site near Hastings

SL - slope

SR - Shaw Road highbush site near Hastings

SRE - sexual reproductive effort

SYCA - sequential yield component analysis

USDA - United States Department of Agriculture

VRE - vegetative expansion

W - statistical measure of component interactions

WD - Woods lowbush site near Fife Lake

X - matrix of independent variables

X - population mean

Y - matrix of dependent variables

YS - Yankee Springs lowbush site near Hastings

INTRODUCTION

Agricultural productivity in the United States of America is rivaled nowhere in the world. Ample resources in the form of water, inexpensive fertilizer, and loamy soils coupled with a moderately long growing season and temperate climate contribute to the high output of agricultural products.

Perhaps surprising is the fact that food production is on tenuous ground because of the lack of a less apparent resource - genetic variability. The expanding population requires increasingly more land for housing and farming and subsequently, the wild germplasm which forms the basis of major food crops is being destroyed at an alarming rate.

The genetic uniformity of our major crops is quite high. Two varieties of sugarbeet account for 42% of total production. Comparable data for corn, potatoes, rice, soybeans and wheat are 6 and 71%, 4 and 72%, 4 and 65%, 6 and 56%, and 2 and 50%, respectively (Reynolds 1975). Although the vulnerability of these crops to diseases and environmental perturbation is tremendous, wild germplasm is usually poorly described and has rarely been intensively studied.

The highbush blueberry is a minor crop species, but typifies the situation in major crops. Most of the genes in 63 commercially released cultivars originated from only three wild selections (Hancock and Siefker 1982). This has resulted in inbreeding depression and limited adaptability. Fortunately, the situation in blueberries differs from major crops in two important ways. First, blueberries grow in bogs or on poor, sandy soils so very little of its original habitat has been modified for housing or farming. Second, the blueberry is one of few crops endemic to North America. For these reasons, the germplasm pool can be examined extensively on a local basis.

Blueberry breeders are now aware that wild germplasm must be incorporated into the genepool for steady improvement to be realized (Ballington 1979, Draper 1977, Hellman and Moore 1983, Lyrene 1983). However, an understanding of how various factors interact to influence growth and reproduction is necessary before a systematic approach to the problem of genetic uniformity can be addressed. The goal of this research is to provide some insight into genetic, morphological, physiological and environmental factors which influence growth and reproduction in wild blueberry populations. This information could then be used to improve production of cultivated material.

Little information is known about how the environment influences blueberry growth and development. Coville (1910) established that blueberries require an acid soil within the range of pH 4.3 to 4.8 for optimal growth. Plants grown on soils outside this range exhibit nutrient deficiency symptoms. Ballinger (1966) has found that blueberries require lower levels of potassium and phosphorus than most other plant species. Light intensity is known to affect flower bud development, growth (Hall 1958) and photosynthetic rate (Forsyth and Hall 1965). Temperature affects germination, pollination and chilling (Gilreath and Buchanan 1981, Hall, Aalders and McRae 1982) and water status is related to normal growth and productivity (Davies and Johnson 1982). However, the specific responses of the plants to these environmental parameters vary across cultivar and species. The genetics of physiological characteristics and their response to environmental parameters are largely unknown.

The first systematic attempt to access genetic variability in highbush blueberries was undertaken by F.V. Coville of the U.S.D.A. He enlisted the help of Elizabeth White who rewarded anyone bringing her superior wild bushes from the New Jersey Pine Barrens. Coville's work resulted in the release of 30 cultivars. George Darrow of the U.S.D.A. and Stanley Johnson of Michigan continued a program of interspecific hybridization and first reported on the inheritance of certain morphological characters (Moore 1966). Camp (1945) constructed a taxonomic key of the genus *Vaccinium* based, in part, on the work of Darrow and Johnson. The taxonomy was later revised by Van der Kloet (1980, 1983), and is still in contention due to the "lumping" of several different ploidy levels into one species. Nonetheless, little effort has been made to measure genotype-environmental interactions involving components of growth and reproduction.

Blueberry breeders must spend considerable time and effort in obtaining desirable genotypes through conventional breeding techniques. However, wild populations of blueberries may have already evolved horticulturally desirable traits. Evolutionary ecologists have observed differentiation of components of growth and reproduction in response to environmental parameters in many species. If these general patterns also hold for blueberry species, a breeder may be able to obtain desirable genotypes simply by choosing individuals from specific environments. Much of the cumbersome methodology involved in plant breeding could then be avoided.

The objective of this study was to describe the patterns of growth and reproduction in the wild populations of sexually compatible species located in Michigan, the highbush blueberry (Vaccinium corymbosum L.) and the lowbush blueberry (V. angustifolium Aiton.). These patterns were then compared to those of other species and theoretical predictions. Ultimately, the environmental parameters responsible for the observed patterns were identified and relationships with other parameters established.

This dissertation is divided into four chapters. The first is a review and discussion of analytical methods used for quantifying complex relationships among components of growth and environment. The second chapter describes the pattern of growth and reproduction of a wild highbush blueberry plant, and discusses relationships among components of yield. The third chapter describes growth and reproduction in the lowbush blueberry, and quantifies phenotypic responses to environment. The fourth presents information on genetic variation in lowbush populations and the influence of environment on differentiation. This study is intended for 1) those interested in genetically improving blueberry cultivars while avoiding problems associated with genetic uniformity, 2) those seeking a better understanding of the growth, reproductive and general life history patterns of woody plant species and 3) those interested in phenotypic and genetic responses of populations to environment.

CHAPTER ONE - The analysis of complex traits in botanical research

I. Introduction

The purpose of component analysis is to identify the simple relationships which form the basis of a complex phenomenon. A greater understanding of a complex trait is attained by quantifying relationships among its components (Williams 1959, Malmborn 1967). The importance of component analysis was realized by plant breeders in the early 1900's. They noted that responses of yield to selection were very complex and unpredictable. Engledow and Wadham (1923) suggested that selection on the components of yield (e.g. number of ears per unit area, number of spikelets per ear, number of kernels per spikelet, kernel weight) would be more efficient than selection for yield itself (kernel weight per unit area). They reasoned that components reflect smaller genetic units than the complex trait; therefore, heritability of individual yield components should be higher than the heritability of yield. This hypothesis was supported by a number of workers in a variety of agronomic crops, and has led to a better understanding of reproductive behavior (Grafius 1956, Leng 1963, Rasmusson and Cannell 1970, Aryeetey and Laing 1973, Jones, Peterson and Shanchez-Mongue 1983).

Workers in other botanical disciplines also encounter complex phenomenon in many aspects of their work. Unfortunately, many are not aware of available methods for analyzing relationships among components of complex traits. Here some statistical techniques of component analysis are briefly described and several areas of research which benefit from these methods are discussed.

II. Methods of Component analysis

A. Correlation

Probably the most common type of analysis used to measure component relationships is correlation. A correlation coefficient is a relative measure of association between any two variables, and ranges from -1.00 to 1.00. Correlation coefficients are independent of the units of measurement and, therefore, are dimensionless. One must be cautious, however, when interpreting them. Components are often measured as ratios, and negative correlations between ratios do not necessarily indicate component compensation. Negative correlations can arise between fractional variables simply because one is an inverse function of another and changes in individual variables are not parallel. Also, an individual component may positively affect some trait, but it may be associated with other components which negatively affect the same trait. Because components act multiplicatively, one cannot conclude from the resulting non-significant correlation coefficient that the individual component is not an important influence.

B. Multiple regression

Multiple regression is frequently used to identify variables strongly associated with a complex response. This type of analysis has been employed by plant breeders to isolate the components of growth and reproduction which most accurately predict yield (Johnson and Schmidt 1968, Lesbock and Amaya 1969, Reddi, Heyne and Laing 1969, Kaltsikes 1973, Ahmed 1980). However, two major problems can arise due to the nature of component data: 1) components are often measured in different units, and this makes regression coefficients difficult to interpret and 2) strong associations between components (multicollinearity) can force the variance-covariance matrix towards singularity and destabilize regression estimates (Kaltsikes 1973, Fakorede 1979, Thurling 1974). Ridge regression, sequential yield component analysis and path analysis have been developed to alleviate these problems.

1. Ridge regression - In ridge regression, variables are standardized by centering them on zero and dividing them by the standard deviation. The ordinary least squares estimate of the regression coefficients is modified to include a bias factor k so that $\beta(k)=(X'X + kI)^{-1} X'Y$ where X and Y are the matrix and vector of standardized variables. The bias factor introduces stability to the estimates while decreasing predictability. The partial regression coefficients $\beta(k)$ are plotted against several bias factors in what is termed a "ridge trace". A bias factor is then chosen which stabilizes the regression estimates without unduly affecting R^2. Variables exhibiting low coefficients or remain unstable are not considered to be associated with the independent variable (Hoerl and Kennard 1970, Draper and Smith 1981).

2. Sequential yield component analysis (SYCA) - SYCA was developed by Eaton and coworkers (Herath and Eaton 1981,

Lovett Doust and Eaton 1982, Lovett Doust, Lovett Doust and Eaton 1983). Yield component variates are introduced sequentially as independent variables into a multiple regression equation predicting a yield variate. The variates are created from a series of transformations and reparameterizations. First, yield component variables are ordered in sequence of development and log transformed. The second transformed variable is made orthogonal to the first by a reparameterization. The orthogonalization forces the covariance between the first two variables to zero. This reparameterization process proceeds sequentially for each additional variable until the covariances between all independent variables are zero. These orthogonalized variates are then standardized by dividing them by their standard deviation. The dependent variate is calculated by summing the independent standardized variable.

Each independent standardized variate is introduced into a multiple regression model in sequence. The incremental increase in R^2 as each variate is introduced is the estimate of the effect of the corresponding yield component on yield. The analysis proceeds by orthogonalization in developmental sequence (forward SYCA), or in reverse (backward SYCA). "Forward SYCA measures the direct and indirect influences of components on yield after all the effects of earlier components have been considered. Backward SYCA measures direct effects of components on yield after they have been influenced by earlier components" (Bowen and Eaton 1983).

3. Path analysis - Sewall Wright (1921, 1934) developed path analysis to separate correlation coefficients into direct and indirect effects. The direct effect is the influence of one component on another without considering interaction between components. The indirect effect is the difference between a correlation coefficient and direct effect, and it measures how components interact to influence the complex trait.

Three steps are involved in the development of a path analysis. First, the components of a complex characteristic are identified which interact either additively or multiplicatively. Multiplicative data are log transformed for linearization. Secondly, the causal relationships (paths) among components are determined. Finally, the standardized partial regression coefficients (β-weights, path coefficients) are calculated for each path of the system. The direct effect of an individual component on another component is equivalent to the path coefficient from a partial model with the latter component as the dependent variable. Models can be expanded to include the secondary components (e.g. leaf area, leaf number) which affect the primary components of yield (Duarte and Adams 1972).

C. W-statistic

Components do not always behave as independent attributes and it is often useful to quantify the overall relationship among components. Hardwick and Andrews (1980) described a statistic which compares the sum of standard deviations of log-transformed components to the standard deviation of the complex trait. This statistic is transformed so that it ranges between 0.0 and 1.0. Compensation, independence or additivity is indicated by the value of this statistic, W. Component compensation (a perponderance of negative correlation or path coefficients) is indicated if W approaches 0.0; 0.5 indicates independence (a balance between negative and positive coefficients) and 1.0 indicates additivity (a preponderance of positive coefficients).

D. Factor analysis

Considerable information can be obtained from analyses in which the dependence structure is known, but many situations arise where causal relationships have not been determined. In factor analysis, a large number of correlated variables is reduced to a smaller number of factors regardless of dependencies involved. This analysis creates groups of related components (factors) which are independent and orthogonal to other groups of related components (Harman 1967). Components within a group covary together, while components in different groups vary independently. Often a factor analysis will allow one to determine the dependence structure of a data set. This can be important when data consist of both physiological and morphological measurements.

E. Comparison of methods

Path analysis, SYCA and ridge regression can all be used to measure the effects of individual components on a complex trait, but SYCA is more cumbersome mathematically because of the increased use of transformations and orthogonalization. Also, any variable included in SYCA must be expressed as a ratio, regardless of its physiological or morphological significance. In addition, components must be forced sequentially into a model even if development occurs simultaneously (e.g. leaf area and leaf number). Ridge regression loses predictive value as bias is added to models. Both ridge regression and path analysis generate a large number of partial regression coefficients, whereas the *W*-statistic concisely summarizes the overall interaction among components. The latter, however, cannot distinguish between a group of non-significant interactions and strongly offsetting interactions. Factor analysis does not require that the dependence structure of the data be known, but it cannot be used to separate direct and indirect effects (Table 1).

III. Applications in botanical research

A. Breeding

1. Direct selection for high yields - Component analysis can be used to identify those components most strongly associated with yield, and these can then be selectively enhanced. This technique may be especially useful to woody plant breeders when components do not change with plant age. Strong component associations may allow yield potential to be estimated at an early age and decrease general time.

The most popular method for analyzing component relationships has been correlation analysis (e.g. strawberries:

Table 1. Comparison of various statistical methods used in the analysis of component data.

Technique	Dependence structure must be known	Transformation required	Standardization required	COMMENTS: Advantages	COMMENTS: Disadvantages
Multiple regression	X			Direct predictive value, can be used for hypothesis testing, is widely used	Interpretation of regression coefficients is difficult, problems arise with multicollinear data
Ridge regression	X		X	Can accomodate multicollinear data, regression coefficients are stabilized and comparable	Regression coefficients contain some bias, choice of bias factor is subjective, loss of predictability
SYCA	X	XX	X	Can accomodate multicollinear data	Mathematically cumbersome, several transformations required, interpretation of results is very subjective, cannot be used for hypothesis testing or direct prediction
Path analysis	XX	X	X	Concise summarization of component interactions, unambiguous interpretation	Requires extensive knowledge concerning the dependence structure of the data set, all sources of variation must be accounted for, cannot be used to make direct predictions
W-statistic	XX	X		Concise summarization of component interactions	Cannot distinguish between overall non-significant interactions and strongly offsetting interactions
Factor analysis			X	Requires no knowledge of dependencies, can accomodate multicollinear data, concise summarization of patterns of variation	Patterns may not be relevant to actual situations, factors require subjective interpretation, cannot be used for prediction or hypothesis testing

Pickett 1917, Morrow, Comstock and Kelleher 1958, Holdelmann 1965, Hanshe, Bringhurst and Voth 1968, Spangelo, et al. 1971, Lacey 1973, Guttridge and Anderson 1973, Mason and Rath 1980). Path analysis has also been used to identify those components having strong direct effects on yield. This analysis has been successful in field crops (Dewey and Lu 1959, Adams 1967, Duarte and Adams 1972, Bhatt 1973, Pandey and Torrie 1973, Thurling 1974, Grafius, Thomas and Barnard 1976, Kang, Miller and Tai 1983), but has only recently been applied to horticultural crops (Ranalli, et al. 1981, Hancock, Siefker and Schulte 1983, Pritts and Hancock 1985a). For example, Shasha'a, Nye and Campbell (1973) used path analysis to demonstrate that pollinator activity was not the cause of low seed yield in 6 lines of onion; rather low yields could be attributed to the percent of flowers developing viable seeds. Seed failure resulted after pollination occurred. These two factors remained confounded until this study.

SYCA has been used by G. W. Eaton and coworkers to identify components most strongly associated with yield. The number of flowering uprights and fruit set made the greatest contribution to yield in cranberry (Eaton and MacPherson 1978, Eaton and Kyte 1978, Shawa, Eaton and Bowen 1981) and seed size and head number were the major components of yield in white clover (Huxley, Brink and Eaton 1979).

2. Selection for yield stability - Component analysis has also been used to aid in breeding for yield stability.

Real (1980) demonstrated that negative covariance among components of a trait acts to buffer the trait. One component can be extremely variable, but if sufficient covariance exists with other components, total yield will still exhibit low variation.

While such negative covariation (component compensation) appears to have a positive effect on yield stability, it can also result in a yield plateau (Lacey, et al. 1983, Way, et al. 1983). Fortunately, not all genotypes with high stability exhibit low yields. Heinrich, Francis and Eastin (1983) accessed the stability of 6 genotypes of sorghum by regressing performance of one particular genotype against the mean performance of the collection of genotypes across a range of environments (Yates and Cochran 1938). Their analysis indicated that high yield potential and stability were not mutually exclusive. In addition, heads/m^2 and seeds/head were highly correlated with yield, but not with each other. Maintenance of high levels of yield components contributed more to stability than compensation among components. According to their data, breeding for increased numbers of seeds/head and greater head weights would improve yield and maintain stability. Several other workers have used regression analysis to identify high yielding, but stable genotypes (Finlay and Wilkinson 1963, Eberhart and Russell 1966, Rod and Weiling 1971, Baihaki, Stucker and Lambert 1976, Gama and Hallauer 1980, Becker 1981, Beaver and Johnson 1981).

Hardwick and Andrews (1980) suggested that breeders select genotypes which tend to exhibit independence or additivity among components using the W-statistic. These genotypes may not encounter a yield plateau as would those exhibiting compensation. Little research has been done on this possibility, although Pritts, Siefker and Hancock (1984) found that W appears to have a genetic component and is related to yield in blueberries.

3. Indirect selection for yield - Numerous physiological and morphological parameters influence yield through their effect on individual components of yield. These can be isolated with component analysis and improved through breeding. Borojevic and Williams (1982) examined yield component interaction in wheat with ridge regression and path analysis. Leaf area index and leaf duration were positively correlated with number of spikes/m^2, but only leaf duration showed a direct effect on grain yield for each of three cultivars over a ten year period. All other direct effects were cultivar specific. Williams, Qualset and Geng (1979) also used ridge regression to identify variables associated with yield in soybean.

Hobbs and Mahon (1982) examined variation and heritability of seven physiological characters in 25 genotypes of peas. CO_2 exchange rate alone would result in increased yield because of its positive association with relative growth rate and harvest index.

Many workers have also used factor analysis to better understand the dependence structure of yield components

(Eaves and Brumpton 1972, Gale and Eaves 1972, Walton 1972, Fakorede 1979, Ottaviano, et al. 1975, Lee and Kaltsikes 1973). Walton (1971) determined which physiological parameters were most strongly associated with yield components in wheat. Spikelets/head and heads/plant were associated with days to maturity, extrusion length with flag leaf area, kernel number with head length and kernel weight with seed filling period. He reasoned that yield improvement would occur through selection on either physiological or morphological components. His analysis also identified the components which could be selected to minimize compensation. For example, a compensatory relationship between spikelets/head and heads/plant could be eliminated simply by selecting for increased days to maturity.

Denis and Adams (1978) used factor analysis on 22 yield determining traits in 16 cultivars of dry beans. Three principal factors were extracted representing size, number and architecture. These factors were interpreted under the construct of source and sink, and led to the development of a high-yielding ideotype. Harmsen (1983) used factor analysis to determine the patterns of covariation among developmental components of *Phaseolus vulgaris*. The first factor contained developmental components which have all been reported to be regulated by auxin.

4. *Estimating genetic relatedness* - The degree of relatedness among genotypes with unknown pedigrees can be approximated with factor analysis. The analysis can reveal

clusters of morphologically similar phenotypes when plotted against the two major principal components. Genotypes within a cluster are likely related. This information can then be used to exploit hybrid vigor or minimize inbreeding depression. In addition, characters whic consistently covary or co-occur may indicate the occurrence of linkage or pleiotropy.

This approach has been used infrequently by horticulturists even though it is commonly employed by taxonomists. Adams (1977) used principal components analysis to calculate genetic distances between cultivars of dry bean. These distances were highly correlated with known genetic relationships based on pedigrees, and were used to determine the vulnerability of production regions to a disease epidemic. Jensen and Hancock (1982) examined wild populations of strawberries and found strong associations between collection site and morphology.

B. Cultural Research

Component analysis can provide a concise summarization of the effects of pruning on fruit size, number and regrowth without extensive tables of correlation coefficients. Neumann and Neumann (1973) used path analysis to measure the effect of pruning on current and future yield components in 2 cultivars of apple. They reported that vegetative characters have strong direct effects on reproductive characters. New shoot growth negatively affected yield through an indirect effect on inflorescence number, while inflorescence number had only a small effect on subsequent shoot growth.

Reports on the effect of thinning on the relationships between fruit numbers, size and yield are often contradictory (Forshey and Elfving 1977), but this can be partially attributed to cultivar differences. For example, thinning resulted in a yield decrease for the grape cultivar 'Thompson Seedless' (Weaver and Pool 1968), but no effect was detected for 'de Chaunac' over a 15 year period (Fisher et al. 1977). A comparison of path coefficients between two cultivars differing in such a response has not been done, but it might indicate a simple physiological or developmental basis for the difference (e.g. leaf/fruit ratio). A similar stragegy provided important physiological information during the selection of high yielding cereal cultivars (Yoshida 1972, Evans and Wardlaw 1976).

Component analysis could also serve as a measure of competition to test the effects of density. Competition is usually assumed to be proportional to density, but the plant's perception of density is difficult to determine. Yield components are thought to exhibit compensation as resources become limiting and, therefore, the relationship between components and density can provide a sensitive measure of stress imposed by different spacing regimes. Adams (1967) found that negative correlations among reproductive components in closely spaced navy beans disappeared at further spacings. Hardwick and Andrews (1980) suggested that the effect of density on these types of interactions be evaluated with their W-statistic.

C. Analysis of Growth and Development

1. Environmental influences - Component analysis can be used to isolate the morphological constituents of yield most affected by environmental variation. SYCA has been used in this context in blueberries (winter cold) and strawberries (boron levels) (Bowen and Eaton 1983, Neilson and Eaton 1983). Pritts and Hancock (1985b) used factor analysis to identify the environmental parameters which most strongly influenced components of growth and reproduction in lowbush blueberries. A principal component analysis identified related groups of environmental variables and growth parameters. The relationships between groups were then determined through correlations of principal component factors.

Ghaderi, Adams and Saettler (1982) used canonical variate analysis, a type of factor analysis, to cluster 39 dry bean cultivars based on the phenotypic response of yield components to 7 environments. Cluster X environmental interaction accounted for 80% of the total genotype X environmental interaction. They reported that two clusters could possess almost identical mean yields, but deviate in opposite directions over the range of environments. Results implied that if the behavior of one cultivar is known, the behavior of all members of the same class would also be similar.

2. Growth analysis - The analysis of growth usually does not consider variability in data (Hunt 1978). However, Elias and Causton (1977) found that variability had a profound effect on the order of the polynomial fitted to observations.

Component analysis offers a unique way to examine variation in growth once the growth function is defined. Karlsson, Pritts and Heins (1986) used path analysis to quantify the relationships among developmental phases in *Chrysanthemum morifolium*. They developed a model of plant growth analogous to one in which yield components interact to produce yield. Total plant dry weight at flowering and dry weight accumulation during phases of development were shown to be mathematically equivalent to yield and yield components, respectively. They found that dry matter accumulation prior to inflorescence bud formation had the greatest influence on final dry weight. In addition, environmental conditions which accelerated growth also delayed inflorescence development. These results indicated that high quality chrysanthemums could be produced more rapidly by changing conditions at the appropriate stage of development, rather than maintaining constant conditions from planting to flowering.

Maddox and Antonovics (1983) used a combination of factor analysis and path analysis to measure the direct and indirect effects of leaf area on reproduction in two species of *Plantago*. Their approach used factor analysis to create leaf area and reproductive variates from measurements of leaf size, leaf number, seeds per plant and seed weight at eight stages of growth. Path analysis was used to measure the effect of leaf area at one stage on leaf area at the next stage, and on both leaf area and reproduction during flowering.

Jolliffe, Eaton and Lovett Doust (1982) used a modified form of SYCA to analyze the growth of bush bean, Phaseolus vulgaris. The incremental increase in the coefficient of determination contributed by various orthogonalized, standardized growth parameters to total plant weight was calculated. The largest increments in R^2 at final harvest were due to leaf dry weight per plant/number of branches per plant and total dry weight per plant/leaf dry weight per plant, but the significance of the various components differed depending on harvest date.

3. Elucidation of metabolic pathways - Many biochemical and physiological processes are also conformable to component analysis although this approach has not been taken with them. For example, the synthesis of certain biochemical compounds occurs through a series of enzymatically regulated steps. Often the activity of one enzyme is regulated by the concentration of a product from another enzyme in the pathway. A hypothetical model of enzyme regulation could be developed using path analysis by introducing various concentrations of substrates of each of the enzymes into the system and monitoring production of intermediates and product. This analysis would give some indication of the type and direction of the regulation, and the compounds and enzymes involved. Component analysis would be useful in any system where component variables are easily measured, but difficult to control (e.g. hormone interactions, gas exchange, water relations, ethylene production).

IV. Conclusions

While the statistical techniques of component analysis are rather sophisticated, they can be applied to a variety of questions that interest plant scientists. The potential applications are certainly not limited to those contained herein. Much data on components of complex phenomenon already exist in the literature, and re-examination of existing data may be well worth the effort. These methods are presented for those interested in obtaining a greater understanding of the complex aspects of plant growth and development.

CHAPTER TWO - Lifetime biomass partitioning and yield component relationships in the highbush blueberry, *Vaccinium corymbosum* L.

I. Introduction

The effect of selection on reproductive patterns has been the subject of extensive theoretical and experimental consideration. Early theory predicted that the mode of population regulation accounted for variation in life history patterns (MacArthur and Wilson 1967, Pianka 1970). Results from tests of this theory suggested that trophic level, environmental predictability (Wilbur, Tinkle and Collins 1974) and age specific mortality (Charlesworth 1980) were also important. Recently, theorists have stressed the influence of environmental variation on life history patterns (Caswell 1983, Kaplan and Cooper 1984, Lacey, et al. 1983, Real 1980), but tests have principally been conducted with short-lived organisms. Long-lived species have generally been ignored, undoubtedly because of size and time constraints; however, perennials may face much more environmental variation than annuals because their resources can vary both within and between years.

The objective of this study was to examine the dynamics of reproduction on a seasonal and lifetime basis in a long-lived woody perennial. The highbush blueberry, *Vaccinium corymbosum*, was selected because it possesses characteristics which make it amenable for such a study. *V. corymbosum* is long-lived but of manageable size. Reproductive organs develop over an 11 month period and are clearly distinguishable from vegetative tissues. In addition, V. corymbosum rarely reproduces vegetatively. These characteristics allow reproductive patterns to be accurately measured.

Several questions were considered in this study. 1) Is reproductive effort in V. corymbosum consistent with the low values predicted by Harper, Lovell and Moore (1970), Gadgil and Solbrig (1972) for woody species? 2) Does reproductive effort continually increase with age as predicted by optimality models (Schaffer 1974, Charlesworth 1980)? 3) Are there indications that V. corymbosum is adapted to seasonal and annual variability in the environment?

A. Species description

Vaccinium corymbosum is a woody, deciduous, perennial shrub. Flower buds develop on two year old wood beginning in late august. Flowering usually occurs in early spring before vegetative bud break. V. corymbosum is self-fertile but requires a pollinator for fertilization to occur. Fruits ripen throughout the summer beginning in July and leaf abscission occurs in late fall as dormancy ensues (Eck and Childers 1966). V. corymbosum is a crown former and propagules rarely develop from underground tissues (Van der Kloet 1980). In Michigan, the highbush blueberry is confined to the southern portion of the state where it occurs on hummocks in acidic bogs.

II. Methods

To measure lifetime reproductive patterns, data must be collected on annual biomass partitioning and growth rates of individual plants of different ages. The relationship between age and partitioning can then be determined and this information can be integrated into a model of lifetime partitioning.

A. Estimation of plant biomass

Eleven V. corymbosum plants ranging in size from 3 to 30 canes were randomly selected from 4 populations (Table 2) in Ingham and Barry counties, Michigan in September 1981. Plants were carefully excavated and separated into leaves, canes (woody stems) and roots. The height and basal diameter of each cane were measured and the roots were washed to remove soil particles. Component plant parts were placed in paper bags and dried in a forced air oven at 80C for one week prior to weighing. A stepwise deletion procedure (Draper and Smith 1981) was then used to generate equations for predicting the biomass of plant parts from non-destructive measurements of cane size and number.

B. Estimation of growth rate

Three plants were randomly selected from each of four populations in November 1981. All canes were cut at ground level and basal diameter, height and number of annual rings were recorded. Cane growth rates for each plant were estimated as the regression coefficients of basal diameter and cane height on age.

Table 2. Locations of *V. corymbosum* populations in southern Michigan.

Site	County	Township-Range	Section
DV	Ingham	T.2N-R.1E	29
GL	Barry	T.3N-R.9W	31
OLS	Barry	T.3N-R.9W	31
SR	Barry	T.3N-R.9W	31

C. Annual partitioning patterns

The following spring (March 1982) a total of twelve plants of various ages were selected from four populations and each cane in the plant was marked and measured for height and basal diameter. The number of inflorescence buds on each cane (buds/cane) of each plant was counted. The number of flowers in 20 randomly selected buds per plant (flowers/bud) was determined after bud break. The percent fruit set (% fruit set) of these 20 buds was determined in July, 1982, after the fruit began to ripen. Mean berry weight per plant (berry weight) was determined from a random set of at least one hundred fruits from each plant. Cane heights and diameters were again measured on the marked individuals in the fall of 1982. This procedure was repeated during the 1983 growing season.

The data on cane size and number were used to estimate vegetative biomass production with the regression equations generated in 1981. Annual vegetative production was determined by subtracting the spring and fall biomass estimates of each of the 12 plants marked in 1982. Annual fruit production was considered to be the product of the yield components for each individual. Annual partitioning patterns could then be expressed as a percentage of annual production. These procedures were repeated in the 1983 growing season.

The relationships between age, allocation patter and growth were used to determine the lifetime pattern of biomass partitioning of a hypothetical plant. This hypothetical plant represents a composite of data derived from measurements on 35 individual plants of various ages and sizes.

D. Seasonal relationships between components of fruit production

The relationships among components of fruit production (yield components) within a season were quantified using path analysis on log transformed data. This analysis allows the partitioning of correlation coefficients into direct and indirect effects. A path coefficient (standardized partial regression coefficient, $\underline{P}$) is a measure of the relationship (direct effect) between two yield components when the influence of related yield components is removed. The sequential development of yield components allows directionality to be assigned to each path coefficient. The significance of path coefficients is determined from F tests (Li 1975, Wright 1921). This technique is applicable when all the components of a system are known.

Yield components may not always behave as independent attributes; therefore, a statistic ($\underline{W}$) was calculated from a function of the variance-covariance matrix for the purpose of quantifying the overall relationship among components (Hardwick and Andrews 1980). A completely independent system of components has a value of $\underline{W} = 0.50$. Values approaching 0.00 indicate compensation (a preponderance of negative path coefficients) and values approaching 1.00 indicate complete additivity (positive path coefficients).

III. Results

The basal radius of canes increased an average of 0.194 cm/year regardless of age. This rate of growth was similar for all plants examined (c.v. = 7.3%). Cane height also increased linearly until age 10 ($r = 0.98$), but no additional increases were detected after this age ($\bar{X} = 180$ cm). The prediction equations based on cane number and size were:

$$\text{Cane biomass} = 1.69\,C^2 - 21.3\,C + .070(\Sigma R^2 H) + 66.4 \quad R^2 = .9998$$

$$\text{Root biomass} = 4.88\,C^2 - 62.1\,C + .146(\Sigma RH) + 179.5 \quad R^2 = .9992$$

$$\text{Leaf biomass} = .709\,C^2 - 6.90\,C + 29.16 \quad R^2 = .9949$$

where C = cane number/bush, R = basal cane radius (cm) and H = cane height (cm).

These equations were used to estimate the annual biomass production of vegetative tissues while the product of yield components was used as an estimate of fruit production. The partitioning patterns were quite variable both among plants and between years (Table 3). For instance, individual annual fruit allocation ranged from 3.9% to 86.3% during 1982 and the coefficients of variation in 1982 and 1983 were 41.8 and 60.9 , respectively. Individuals with low root allocation in 1982 tended to have higher root allocation the following year ($r = -0.71$, d.f. = 7, $p < .05$), but correlations between the allocation of other tissues were not signiicant. No significant association was detected between reproductive effort in 1982 and vegetative growth in 1983 ($r = 0.37$, d.f. = 7), or between vegetative growth in 1982 and reproductive effort in 1983 ($r = 0.28$, d.f. = 7).

Table 3. Means of yield components and annual partitioning patterns for 9 individuals in 1982 and 1983. Coefficients of variation are in parentheses. Three individuals were not included in the tabulations because they were frost damaged in April 1983. Percentages were arcsine transformed prior to analysis. r = correlation coefficient of individuals between years, p = probability that association is due to chance, and d.f. = 7.

COMPONENT	Mean 1982	Mean 1983	r	p
berry weight(g)	.0667 (35.0)	.0567 (29.7)	0.783	0.02
flowers/bud	6.19 (18.7)	5.69 (20.2)	0.583	NS
% fruit set	62.8 (39.2)	81.7 (7.6)	0.494	NS
buds/cane	39.9 (79.1)	32.4 (59.3)	-0.096	NS
cane number	16.9 (70.2)	21.0 (63.2	0.998	0.001
yield (g)	175.46 (114.3)	149.09 (94.0)	0.229	NS
% fruit biomass	46.0 (41.8)	29.7 (60.9	0.602	NS
% root biomass	7.3 (36.6)	33.3 (33.1)	-0.707	0.05
% cane biomass	3.6 (38.4)	11.8 (27.8	-0.572	NS
% Leaf biomass	43.0 (45.6)	25.2 (24.2)	0.563	NS

Figure 1.

Diagram depicting the interrelationships between yield components arranged in developmental sequence for V. corymbosum. Corresponding numbers are path coefficients (P). Asterisk denotes significant relationships between variables at $\alpha = 0.05$.

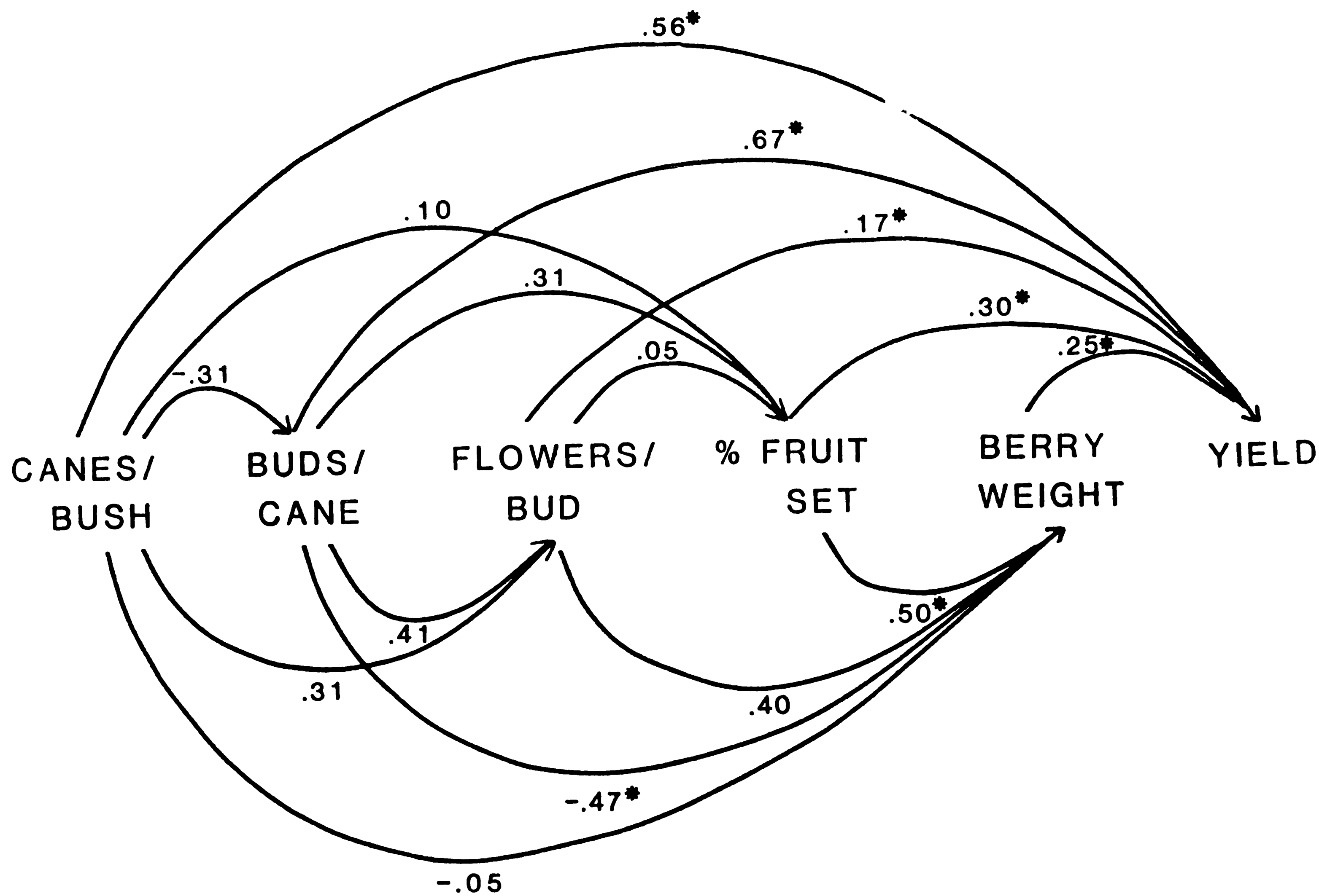

.56*
.67*
.10
.17*
.31
.30*
-.31
.05
.25*
CANES/
BUSH
BUDS/
CANE
FLOWERS/
BUD
% FRUIT
SET
BERRY
WEIGHT
YIELD
.50*
.41
.31
.40
-.47*
-.05

Figure 1

Yield components were also quite variable among plants (Table 3). Berry weight, flowers/bud and canes/plant were significantly correlated between years, but buds/cane and percent fruit set were not. This resulted in high variation for yield among plants and a low correlation between years ($r = 0.23$, d.f. = 7).

The direct effects of individual yield components on yield and reproductive effort were determined with a path analysis (Fig. 1). Data from 1982 and 1983 were combined as no significant differences in path coefficients were found between years. Canes/plant and the number of buds/cane were found to strongly affect yield. Percent fruit set had a positive effect on fruit size while buds/cane had a positive effect on fruit size while buds/cane had a negative effect. Other interrelationships among components were not significant and this contributed to the absence of any significant indirect effects.

Cane number had a negative effect on reproductive effort ($\underline{P} = -0.37$) in contrast to its positive effect on yield ($\underline{P} = 0.56$). Buds/cane and berry weight were also positively associated with reproductive effort($\underline{P} = 0.85$ and 0.50, respectively). Component interaction within the entire system was classified as nearly independent ($\underline{W} = .515$) according to the method of Hardwick and Andrews (1980).

The lifetime pattern of biomass partitioning constructed from annual patterns and growth measurements revealed that individuals between 3 and 11 years old allocated 50% of

Figure 2.

Pattern of biomass partitioning based on the percent of lifetime production allocated to root, cane, leaf and reproductive tissues for individuals of different ages in V. corymbosum.

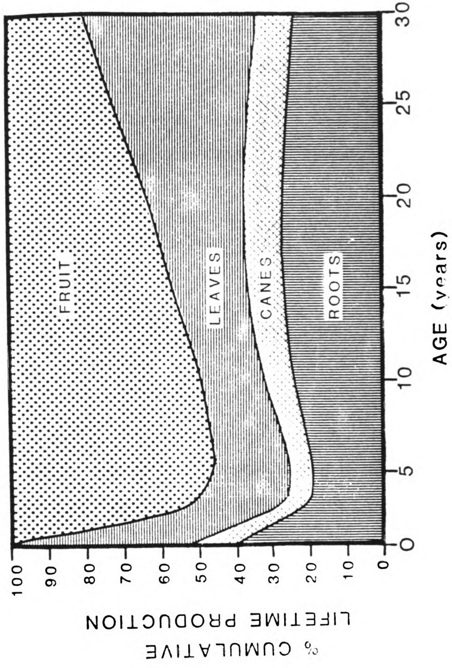

FRUIT
LEAVES
CANES
ROOTS
% CUMULATIVE
LIFETIME PRODUCTION
100
90
80
70
60
50
40
30
20
10
0
AGE (years)
5
10
15
20
25
30

Figure 2

Figure 3.

Amount of annual production in leaf, root, cane and reproductive tissues of *V. corymbosum* as a function of plant age. Left axis denotes vegetative production and right axis denotes fruit production.

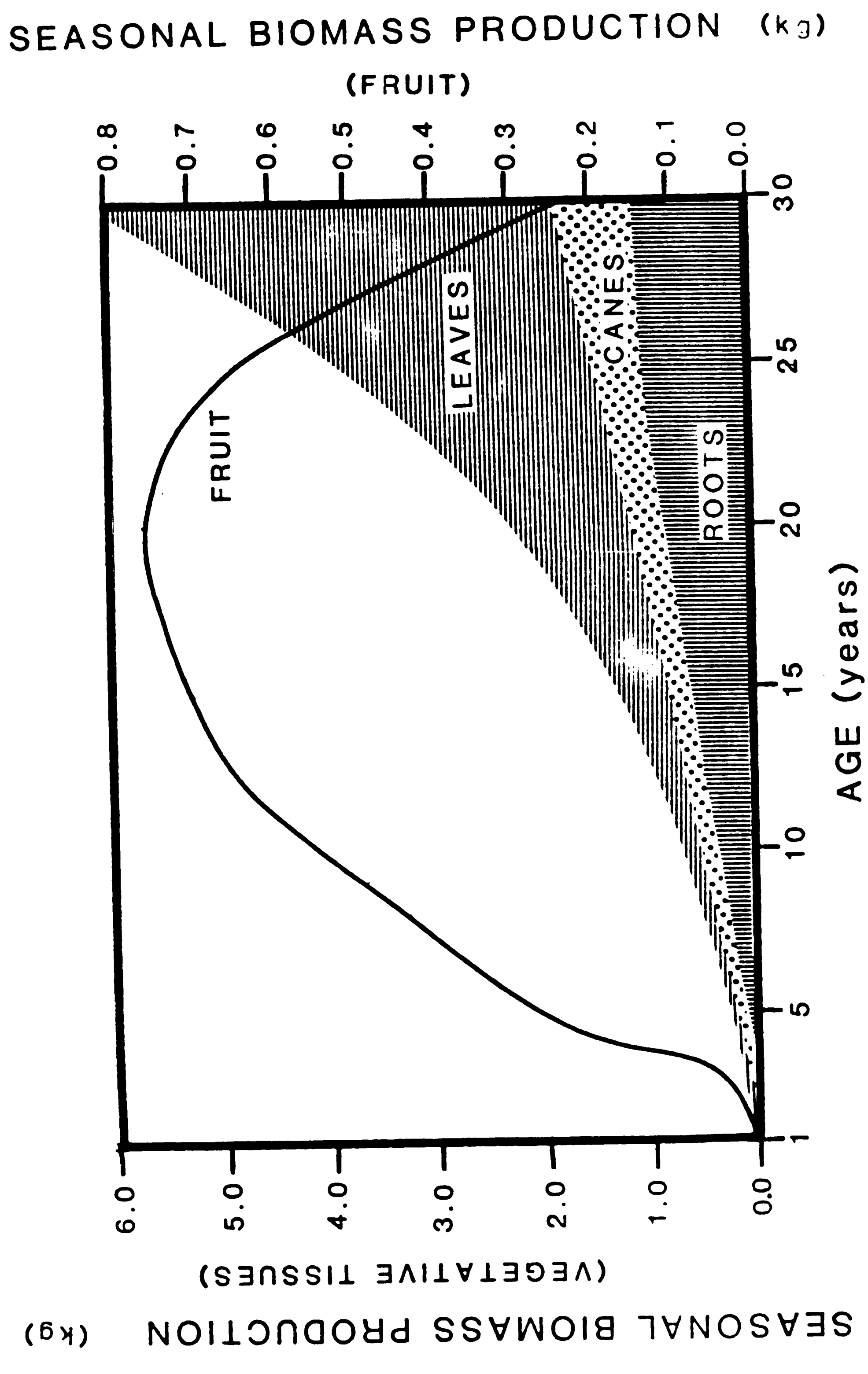
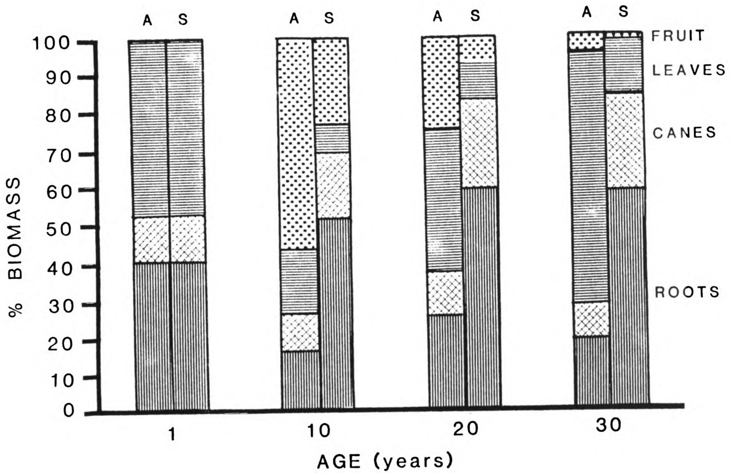

SEASONAL BIOMASS PRODUCTION (kg)
(FRUIT)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
FRUIT
LEAVES
CANES
ROOTS
1
5
10
15
20
25
30
AGE (years)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
(VEGETATIVE TISSUES)
SEASONAL BIOMASS PRODUCTION (kg)

Figure 3

Figure 4.

Comparison of the percentage of annual production allocated to various tissues (column A) with the percentage of standing biomass consisting of the same tissues (column S) for ages 1, 10, 20 and 30 in *V. corymbosum*.



A
S
100
90
80
70
60
50
40
30
20
10
0
% BIOMASS
1
10
20
30
AGE (years)
FRUIT
LEAVES
CANES
ROOTS

Figure 4

biomass production to fruit (Fig. 2). This ratio steadily decreased with age and resulted in a yield decline after age twenty. After this point, leaf allocation exceeded the annual production apportioned to roots and canes. This growth model was used to compare annual partitioning with standing biomass determinations. The difference between estimates of reproductive effort from both methods is quite large in older plants (Fig. 4). For instance, a twenty year old plant allocates 25% of its annual production to fruit which is only 7% of its total biomass.

IV. Discussion

A. Seasonal patterns

Engledow and Wadham (1923) first suggested that an analysis of yield components, rather than yield itself, would improve breeding efficiency in agronomic crops. Tedin (1925) soon reported negative associations among components of yield in *Camelina sativa-linicola* at close spacings. Since then, negative associations have been reported in barley (Rasmusson and Cannell 1970), maize (Leng 1963), wheat (Knott and Talukdar 1971), field beans (Duarte and Adams 1972), soybeans (Pandey and Torrie 1973), navy beans (Adams 1967), and many other crop species. Adams (1967) proposed that plants in natural environments should also experience intraplant competition for resources and this, in turn, would result in negative correlations among yield components.

Few workers have examined the relationships among yield components in natural populations. Data from Hume and Cavers

(1983) revealed no significant correlation between achene weight and numbers among 11 populations of *Rumex crispus*. Maddox and Antonovics (1983) reported three positive and seven nonsignificant correlations among the four yield components in both *Plantago aristita* and *P. patagonica*. Primack (1978) also found that correlations between yield components within populations of *Plantago* species were either neutral or positive. Primack and Antonovics (1981) working with *Plantago lanceolata* detected few negative correlations even under artifically low nutrient conditions and Schall (1980) found no significant negative correlations among yield components in *Lupinus texensis*. Lloyd, et al. (1980) examined the correlations between yield components of 17 species and found them to be generally non-significant. Similarly, this work on *V. corymbosum* detected only one negative path coefficient among the five yield components (buds/cane with berry weight) while the other 9 relationships were either positive or neutral. Overall component interaction in *V. corymbosum* exhibited nearly complete independence ($\underline{W}$ = 0.515). Although the data base is still limited, these findings suggest that independence among yield components is quite common in natural populations.

Independence among yield components may have an important adaptive value in variable environments. Lloyd (1980) proposed that the ability to regulate maternal investment in progeny at discrete stages during the season would be adaptive in environments where resource levels fluctuate seasonally.

A high degree of independence among components would allow regulation of reproduction in response to immediate conditions, regardless of previous yield component development. For example, even if a high percentage of flower buds were destroyed due to a late frost, the plant could still have a high reproductive effort if conditions were favorable for pollination and berry development. Individuals able to regulate reproduction in response to immediate microenvironmental conditions would have the potential to maximize reproduction during favorable conditions, but could also limit reproduction under deteriorating conditions (Janzen 1978, Stephenson 1980, Wyatt 1981, Bookman 1983).

B. Annual patterns

Independence among yield components between seasons may also be adaptive. Individuals unable to exploit high resource levels because of previous environmental conditions would be at a disadvantage relative to others exhibiting independence between years. In V. corymbosum, most of the reproductive traits acted independently between years. A significant correlation in mean berry weight between years was detected, but flowers/bud, % fruit set and buds/cane in 1983 were unrelated to numbers in 1982. In general, annual allocation patterns followed the same trend and there was no relationship between vegetative growth and reproduction in an alternate year. Although suggestive, these patterns must be observed over additional years to adequately test for independence between years.

Hirshfield and Tinkle (1975) proposed on theoretical grounds that year to year changes in reproductive efforts of individuals should be expected in species inhabiting variable environments. The changes observed between years in herbaceous plant populations (Jaksic and Montenegro 1979, Soule and Werner 1980) and within individuals of V. corymbosum confirm this expectation.

C. Lifetime patterns

There has been debate as to the best method of measuring reproductive effort (Thompson and Stewart 1981, Abrahamson and Caswell 1983, Watson 1984). Pritts and Hancock (1983a) demonstrated that the percent of total plant biomass consisting of reproductive structures is not a good estimator of reproductive effort for woody, iteroparous species. Findings on V. corymbosum support this contention. Standing biomass estimates can underestimate reproductive allocation by 75% in older plants (Fig. 4). Others have arrived at a similar conclusion (Sarukhán 1978).

The reproductive effort of V. corymbosum is higher than the range of 10 - 15% predicted by Mooney (1972) for woody plants. Other woody plants also exhibit high reproductive efforts if measured as a percent of annual production. For example, Avery (1969), Maggs (1963) and Forshey et al. (1983) each reported that apple trees allocate greater than 33% of net annual aboveground production to fruit. Whittaker (1962) examined annual reproductive allocation in 7 ericaceous shrubs and found that it ranged from 7% in Rhododendron maximum to 35% in Vaccinium pallidum ($\overline{X}$ = 19.4%). Sharifi et al. (1982) reported values of 34.3% for the shrub Prosopis glandulosa, Cunningham et al. (1979) found values of 15% for Larrea tridentata and data from Buchholz and Good (1982) indicate tht Pinus rigida of the New Jersey Plains allocated 41.3% of annual aboveground production to cones. Pritts and Hancock (1983) determined that Solidago pauciflosculosa allocated greater than 30% of biomass production to reproductive structures over the course of its lifetime. In this study, reproductive allocation in young V. corymbosum individuals exceeded 50%.

These data indicate that the woody growth habit may not always be associated with low reproductive effort. Perhaps the proposed evolutionary trade-off between reproductive and competitive structures does not exist or many woody plants have evolved under the same mortality regimes as herbaceous species.

Charlesworth (1980) suggests that reproductive effort is most likely to increase with age when population growth is low, adult survival is high, and when individuals continue to grow in size during adult life. This prediction fits the allocation pattern of Astrocaryum mexicanum (Sarukhán 1980) and Solidago pauciflosculosa (Pritts and Hancock 1983), but does not fit V. corymbosum. However, other factors can influence these patterns. Older plants may have a greater metabolic load which results in decreased reproductive effort. Also, resources may become depleted in the root zone where the plant is growing. The effect of physiological and environmental parameters on the lifetime allocation pattern requires further study.

Methods for determining the interaction between age and production in woody plants must rely on several assumptions and inferences (Chew and Chew 1965, Van Valen 1975). In the model presented, the assumption was made that equations for predicting plant biomass were accurate for all plants examined in both years. I feel this assumption was justified because coefficients of determination were very high over a 500 fold range of plant weights. Second, I felt that the years in which partitioning was examined were representative of normal conditions. This cannot be completely tested except with long term measurements; however, yield data for commercial plantings were not unusual in 1982 and 1983 (Brightwell and Johnson 1944, Moore 1979). Third, selected plants were assumed to be representative of southern Michigan populations. This was likely as individuals of different ages were delected from different populations, and all populations were located in very similar types of habitats. Fourth, I assumed that cane mortality did not need to be included in the model. Again, long term data does not exist, but I observed little evidence of cane mortality in 1982 and 1983, and few dead canes were detected in any bush. Fifth, loss of biomass through the root system was not considered. Loss of root hairs accounts for most of the biomass removed in systems which have been studied (Caldwell 1979); however, ericaceous plants do not possess root hairs. Sixth, extrapolations were made beyond the range of the sampled data. This may have led to error, but I estimated only for years 1-3 and 26-30 and this would have had little effect on the overall calculated trends. Thus, the lifetime allocations pattern is probably an accurate representation.

In conclusion, *Vaccinium corymbosum* appears to be well adapted to a variable environment. The independence among yield components suggests that *V. corymbosum* has the potential to regulate maternal investment at several discrete stages during reproductive development. In addition, the lack of correlation between years suggests that previous conditions do not affect responses to future conditions. Finally, potential reproductive effort in *V. corymbosum* is very high. These characteristics may be selected in species inhabiting variable environments.

CHAPTER THREE - Independence of life history parameters in populations of *Vaccinium angustifolium*

I. Introduction

Organisms are confronted with finite and often limiting resources at all stages of the life cycle. The allocation of these finite resources to various components of vegetative growth and reproduction has come under theoretical consideration. For example, Gadgil and Solbrig (1972) postulated that density independent mortality acts to increase reproduction at the expense of vegetative growth, and density dependent mortality favors increases in vegetative growth with a concurrent decrease in reproductive effort.

Abrahamson (1975a) extended this theory to include perennials capable of both sexual and vegetative reproduction. He postulated that vegetative reproduction is favored at the expense of sexual reproduction when population density is low, and sexual reproduction is favored at high densities. Harper (1967) also suggested that the organs associated with sexual and asexual reproduction compete for resources within a plant. Kawano (1981), Wilbur (1977) and Werner and Platt (1976) discussed a trade-off within plants between seed size and numbers. Implicit in these and other hypotheses is the assumption that components of vegetative and reproductive growth share the same limiting resources, and this results in negative relationships between components.

Few studies have been designed to measure the relative amount of resource sharing among life history parameters.

Charlesworth (1980) suggested that such studies be confined to populations of the same species to reduce the influence of multiple ecological factors and genetic constraints. In addition, Soule and Werner (1980) and Quinn and Hodgkinson (1984) demonstrated the need to sample multiple populations when studying trends involving life history parameters. The objective of this study was to determine the relative degree of "resource sharing" among life history components in populations of a woody, rhizomatous perennial, Vaccinium angustifolium. Covariation among life history and yield components was accessed in 17 populations observed under various demographic and environmental regimes. The degree of resource sharing was determined from patterns of covariation, and was related to environmental and demographic variables.

A. Species description

Vaccinium angustifolium Ait. is a tetraploid, rhizomatous, woody perennial which inhabits a diversity of environments where the soil is of sufficiently low pH. Seeds germinate in open habitats under high moisture conditions usually after clearcutting or fire (Van der Kloet 1976a). Shoots are produced from rhizomes and remain attached to the mother plant. Extensive colonies can form which remain productive for more than 100 years (Eaton and Hall 1961). V. angustifolium ranges from eastern Canada southward through Minnesota, Wisconsin and Michigan to southern Virginia mountains (Van der Kloet 1978). Flower buds initiate in late summer, followed by leaf senescence and dormancy in October. Flowering usually preceeds vegetative bud break in Late May or June, wild bees pollinate the flowers soon after anthesis, and fruits ripen from July through late August. V. angustifolium is self-fertile but requires a pollinator (Eck and Childers 1966). This species has been reported to have substantial morphological variation (Camp 1945, Van der Kloet 1978).

II. Methods

A. Environmental measurements

Seventeen environmentally diverse sites containing extensive clones of V. angustifolium were selected throughout Michigan (Table 3). Soil samples from each site were collected in July 1982 and analyzed for pH, nitrate, phosphorus, potassium, magnesium and calcium by the Michigan State University Soil Testing Laboratory. Soil moisture content in 5 cm^3 subsamples from 10 cm below the surface was measured during each month of summer in 1982 and 1983. Moisture was determined gravimetrically and reported as the average ratio of (wet weight - dry weight)/dry weight for each sampling date. Moisture readings were highly correlated within a site, so only the measurement during berry ripening was used in subsequent analyses. Available sunlight was expressed as a percent of the photosynthetically active quantum flux density at the site compared to full sunlight during the same sampling period. Twelve readings were taken at random locations in each site in rapid succession to estimate average quantum flux density. Slope, latitude, longitude and distant from the nearest large body of water (Lake Michigan or Lake Superior) were included as environmental parameters.

Table 4. Specific locations of each of 17 *V. angustifolium* populations in Michigan.

Site	County	Township-Range	Section	Latitude	Longitude
BR	Marquette	T.47N-R.25W	28	46.26 N	87.27 W
MB	Alger	T.47N-R.18W	3	46.29 N	86.33 W
LS	Alger	T.48N-R.17W	12	46.35 N	86.22 W
BL	Alger	T.48N-R.16W	18	46.34 N	86.22 W
AT	Alger	T.48N-R.15W	29	46.32 N	86.13 W
GM	Alger	T.49N-R.13W	9	46.39 N	85.53 W
BG	Grand Traverse	T.27N-R.12W	28	44.43 N	85.44 W
OD	Grand Traverse	T.26N-R. 9W	4	44.43 N	85.29 W
WD	Grand Traverse	T.25N-R. 9W	23	44.23 N	85.21 W
CD	Grand Traverse	T.26N-R. 9W	13	44.39 N	85.24 W
CW	Roscommon	T.22N-R. 4W	8	44.18 N	84.51 W
OW	Roscommon	T.22N-R. 4W	17	44.17 N	84.51 W
MD	Roscommon	T.22N-R. 2W	20	44.22 N	84.35 W
MW	Roscommon	T.23N-R. 3W	12	44.23 N	84.38 W
SK	Barry	T. 3N-R.10W	27	42.37 N	85.27 W
NK	Barry	T. 3N-R.10W	27	42.37 N	85.27 W
YS	Barry	T. 3N-R.10W	29	42.37 N	85.30 W

B. Demographic and life history measurements

1. Density, vegetative expansion and percent flowering shoots

Several life history and demographic parameters were measured at each site in 1982 and 1983. Density in early spring was estimated as the average number of individual shoots in twelve 0.25 m^2 circular quadrats at 3 meter intervals along a transect through the center of each population. The percent of shoots which flowered was determined from individuals in this sample. Vegetative expansion (VRE) was determined by tagging all shoots in two 0.5 m^2 quadrats in spring and counting the number of untagged shoots in late fall. The ratio of untagged/tagged shoots was the estimate of VRE.

2. Yield, yield components and reproductive effort per shoot

The basal radius and height of 10 randomly selected flowering shoots were measured in early spring of 1982 and 1983 at each site. Bud numbers were counted for each shoot, and the number of flowers in three randomly selected buds on each of the ten shoots was recorded and marked. The percent fruit set of a particular population was estimated as the average ratio of berry number/flower number for each of the thirty marked buds. Berry weight was determined from a sample of at least 100 ripe berries collected from each site in late July. Ripe berries were oven-dried at 80C for at least one week prior to weighing. Immediately prior to leaf senescence, each of the previously marked shoots was cut at the base and transported to the lab. The basal radius and height were again recorded, and leaves were separated from stems. Leaf and stem tissue was placed in paper bags and oven dried at 80C for at least one week prior to weighing.

Quadrats 0.5 m^2 were selected immediately prior to leaf senescence near the center of three different clones, and all individuals within each quadrat were excavated. These samples were transported to the lab where leaves and soil were removed, and stems were separated from underground tissues and each placed in paper bags and oven-dried as previously described. The stem/root ratio was determined from these samples.

The product of basal radius squared and height of a stem was found to be an excellent predictor of dry weight in lowbush blueberries ($r > 0.95$). The annual productivity of each flowering stem in this study was calculated by first solving the proportionality $r_1^2 h_1/s_1 = r_2^2 h_2/s_2$ for s_1 where s_1 and s_2 are stem dry weights, r_1 and r_2 are basal radii, and h_1 and h_2 are the heights in spring and fall respectively. Annual stem productivity was estimated as the difference between s_2 and s_1. Annual allocation patterns for flowering shoots at each site were then calculated from the stem/root ratio, leaf/stem ratio, annual dry weight increase of stems and berry dry matter production/stem.

3. <u>Clonal reproductive effort, age and size structure</u>

Eight of the 17 sites were more intensively investigated because of the extreme environmental variation represented along a similar latitude. Two 0.5 m^2 quadrats were selected within each population, and all individuals were removed. The age of each stem was determined by counting annual rings, and the corresponding basal radius and height were measured. In addition, 10 non-flowering shoots were marked in early spring of each year, and their basal radius and height recorded. In late fall all marked shoots were cut at ground level and transported to the lab where annual allocation patterns were determined as described previously. The annual partitioning pattern of the entire clone was calculated from partitioning patterns of both flowering and non-flowering individuals, the size distribution of flowering and non-flowering individuals, the size distribution of flowering and non-flowering shoots in the population samples, and the mean weight of each size class.

4. Mortality

The large sizes of individual clones indicated that the sites had been undisturbed for many years; therefore, the frequency of age classes within a clone was assumed to be representative of the survivorship curve of a population. We used the negative regression coefficient of this semilog relationship as a relative measure of mortality. Clonally reproduced shoots experienced equal mortality with respect to age as indicated by strong linear relationships ($r > 0.97$) between age and log of frequency.

C. Statistical analyses

A principal components analysis was performed on the sets of environmental and life history variables using the

SPSS statistical package, type PA1. Percentage data were transformed with square-root arc-sine, and all data were standardized to mean zero and variance one. This technique was used to measure the covariation among parameters of each data set. Each principal component represents a group of variables which covary together. Individual principal components are orthogonal to each other; therefore, groups of related variables are independent. The eigenvalues, factor loadings and factor coefficients (weights) were used to interpret the significance of each principal component. The correlation coefficients between the five major environmental principal components and the five major life history principal components were also calculated.

The interrelationships among yield components were quantified using a path analysis on log-transformed data (Wright 1921, Pritts and Hancock 1985a). Sites experiencing extensive frost damage during any one year were excluded. In path analysis, the investigator develops a diagram depicting all possible interrelationships among components prior to the analysis. Causal relationships in this study are clear as components develop sequentially. A path analysis allows the partitioning of correlation coefficients into direct and indirect causal effects. A path coefficient (standardized partial regression coefficient, $\underline{P}$) is a measure of the relationship (direct effect) between two yield components when the influence of related variables is removed. Direct effects are equivalent to the regression coefficients of standardized variables when the affected component is a dependent variable in a multiple regression model. The significance of path coefficients is determined from F tests (Li 1975).

A statistic (W) was calculated from a function of the variance-covariance matrix to quantify the overall relationship among components (Hardwick and Andrews 1980). A completely independent system of components would have a value of W = 0.50. Values approaching 0.00 indicate compensation (resource sharing), and values approaching 1.00 indicate positive relationships.

III. Results

Sites selected throughout Michigan (Table 4) were quite variable as reflected by the high coefficients of variation (Table 5) and the ordination of principal components (PC's) (Fig. 5). No single group of factors accounted for more than about 1/3 of the total variation (Table 6). An interpretation of each principal component was made from an examination of factor coefficients and loadings. PC1 loaded highly for all nutrients but nitrogen, PC2 appeared to be a location parameter, PC3 represented mostly nitrogen and pH, PC4 loaded highly for light and PC5 loaded significantly only for phosphorus. Other principal components exhibited no significant loadings for any environmental variable.

Life history and yield components were also quite variable (Table 5). Vegetative expansion was the only component which remained stable from one year to the next (Table 7). The major principal component again accounted for only 1/3 of the total variation. This is an extremely low value and

Table 5. Environmental, demographic and life history variables measured in this study followed by their designated abbreviation and coefficient of variation (CV).

Parameter		CV
ENVIRONMENTAL		
% soil moisture	MJ	62
% ambient PAR	PLT	44
nitrate nitrogen	N	21
phosphorus	P	102
potassium	K	60
magnesium	MG	73
calcium	CA	87
hydrogen ion conc.	PH	87
percent organics	PORG	51
slope	SL	163
distance from lake	DW	116
latitude	LAT	2
longitude	LONG	1
LIFE HISTORICAL		
berry number	BN	90
growth per shoot	BPS	26
sex. repro. effort	SRE	33
veg. repro. effort	VRE	71
REPPRODCUTIVE		
buds/shoot	BPS	29
flowers/bud	FB	9
% fruit set	PS	56
berry weight	BW	9
DEMOGRAPHIC		
density	DEN	54
mortality	MT	22
% flowering shoots	PFL	70

Table 6. Factor coefficients (C) and significance of loadings (L) for each environmental variable on the first five principal components. *p<0.05, **p<0.01, ***p<0.001. Loadings are positive unless asterisk is preceeded by a (-). Contribution of each principal component to total variation is listed at the bottom of the columns.

	PC1		PC2		PC3		PC4		PC5	
Variable[1]	C	L	C	L	C	L	C	L	C	L
MJ	-0.14	*	0.03	*	1.10		0.41		0.11	
PLT	0.03		-0.02		0.25		0.56	**	1.53	
N	-0.14		-0.12		0.62	**	1.52		0.55	
P	0.03	-*	0.15		0.50		0.34		0.42	**
K	0.42	*	-0.01		-0.18		-0.08		0.02	
MG	0.38	***	-0.03		-0.15		-0.09		0.01	
CA	0.47	**	-0.04		-0.14		-0.11		0.03	
PH	-0.11	*	-0.01		0.75	-*	0.25		0.08	
PORG	-0.14	**	-0.14		-0.28		0.06		0.07	
LAT	-0.03	*	0.48	-**	-0.02		-0.09		-0.03	
LONG	-0.02	*	0.55	-*	0.01		-0.09		-0.03	
DW	0.05	-*	-0.24	*	-0.06		0.04		0.01	
SL	0.06		-0.13	-*	0.42		0.46	-*	0.65	
% total variation	35.7		22.9		14.3		9.6		6.5	

[1]MJ moisture, PLT ambient light, N nitrogen, P phosphorus, K potassium, MG magnesium, CA calcium, PH acidity, PORG percent organics, LAT latitude, LONG longitude, DW distance from lake, SL slope.

Table 7. Correlation coefficients of yield and life history components between 1982 and 1983. Asterisk indicates significance at $p < 0.05$.

Component	r
sexual reproductive effort	0.255
vegetative reproductive effort	0.909*
percent leaves	0.503
percent underground tissue	0.149
percent stems	0.178
berry weight	0.314
flowers per bud	0.564
percent fruit set	0.284
buds per shoot	0.468
yield	0.158

Figure 5.

Ordination showing the location of each site in relation to the first two principal components of environmental variables. The first principal component had high weights and loadings for nutrients and moisture while the second was a location parameter (See Table 6).

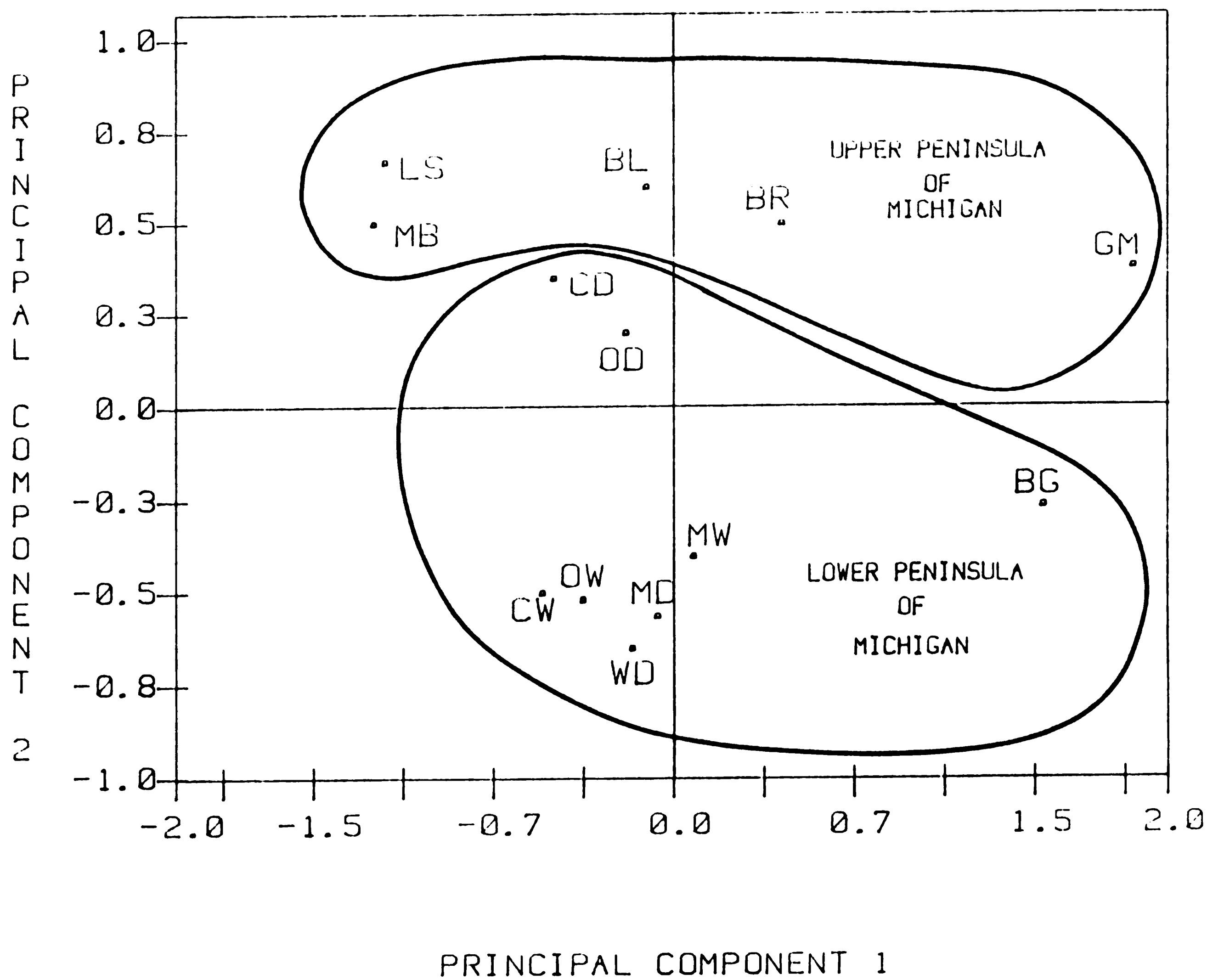

PRINCIPAL COMPONENT 2
1.0
0.8
0.5
0.3
0.0
-0.3
-0.5
-0.8
-1.0
-2.0
-1.5
-0.7
0.0
0.7
1.5
2.0
LS
MB
BL
BR
GM
CD
OD
MW
OW
CW
MD
WD
BG
UPPER PENINSULA
OF
MICHIGAN
LOWER PENINSULA
OF
MICHIGAN
PRINCIPAL COMPONENT 1

Figure 5

could have occurred by chance alone (Karr and Martin 1981). However, the five principal components together accounted for 98.3% of the total variation (Table 8). PC1 had large weights and loadings for vegetative expansion and percent flowering shoots, PC2 for mortality rate and shoot productivity, PC3 for sexual reproductive effort, PC4 for berry number and PC5 for density. Several environmental PC's were highly correlated with these life history PC's (Fig. 6).

The complex traits of yield and reproductive effort were affected by environmental factors even though this was not reflected by the principal component analysis. Yield is composed of several simple traits and these are influenced by independent factors. Bud number/shoot and flower number/bud are correlated with light availability ($r = 0.61$ and 0.49, $p < 0.05$, respectively), fruit set is controlled by pollinator activity and fruit size is correlated with moisture availability ($r = 0.33$, $p < 0.20$). Because these components act multiplicatively, yield is not associated with single environmental factors.

All reproductive components had a direct positive effect on yield/shoot (Fig. 7). In addition, three other positive direct effects were detected among reproductive components. The only negative relationship was between bud number/shoot and berry weight. The overall interaction among yield components was slightly additive ($\underline{W} = 0.726$). _V. angustifolium_ populations allocated an average of 21% of biomass production to fruit across all sites, with a range of 5 to 45%.

Table 8. Factor coefficients (C) and significance of loadings (L) for life historical-demographic variables on the first five principal components. *p<0.05, **p<0.01, ***p<0.001. Loadings are positive unless asterisk is preceeded by a (-). Contribution of each principal component to total variation is listed at the bottom of each column.

Variable[1]	PC1		PC2		PC3		PC4		PC5	
	C	L	C	L	C	L	C	L	C	L
MT	0.05		-0.64	-***	0.03		-0.17		0.26	
VRE	0.54	**	-0.05	*	0.02		0.00		0.11	
SRE	-0.02	-*	-0.02		1.13	*	-0.14	*	-0.25	
BPS	-0.02	-*	0.56	***	0.01		-0.16		-0.24	
PFL	0.59	**	-0.01		-0.06	*	0.02		0.14	
BN	-0.02		-0.20		-0.15	-*	1.15	**	0.26	
BW	-0.06	*	-0.06	*	0.01		0.05		0.04	
DEN	0.15	-*	-0.26		-0.22		0.22		1.32	*
% total variation	33.9		29.0		18.0		12.9		4.5	

[1]MT mortality, VRE vegetative expansion, SRE sexual reproductive effort, BPS productivity, PFL percent flowering shoots, BN berry number, DEN density, BW berry weight

Figure 6.

Relationships between major principal components of both environmental variables and life history traits as determined by correlation for V. angustifolium. Only coefficients significant at $p < 0.05$ are depicted.

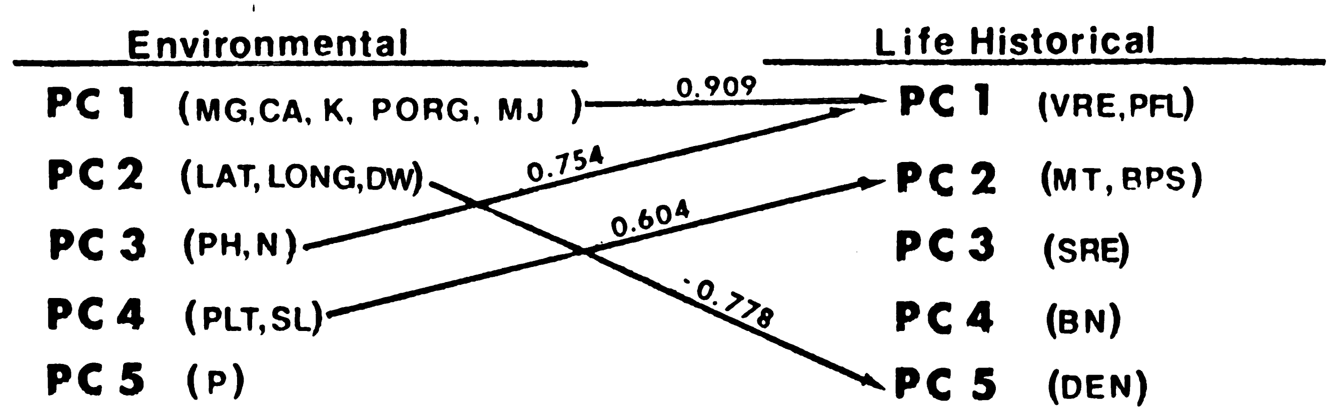

Environmental
Life Historical
PC 1 (MG,CA, K, PORG, MJ)
PC 2 (LAT, LONG,DW)
PC 3 (PH, N)
PC 4 (PLT, SL)
PC 5 (P)
0.909
0.754
0.604
-0.778
PC 1 (VRE,PFL)
PC 2 (MT, BPS)
PC 3 (SRE)
PC 4 (BN)
PC 5 (DEN)

Figure 6

Figure 7.

Path diagram of interrelationships between components of reproduction in _V. angustifolium_. Numbers corresponding to each path are path coefficients (_P_) which are relative measures of direct effects. The significance of each path coefficient is indicated with an asterisk: * $p < 0.05$, ** $p < 0.01$.

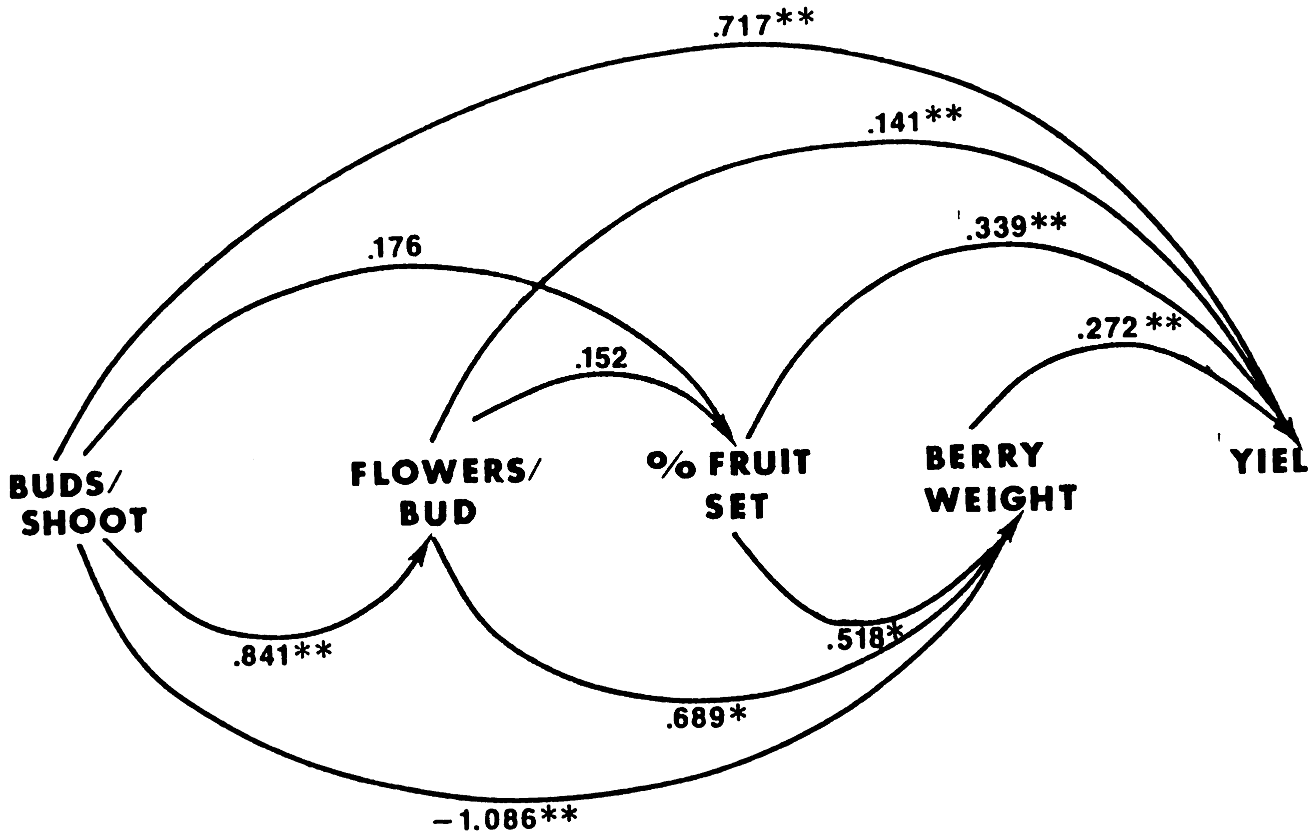

.717**
.141**
.176
.339**
.152
.272 **
BUDS/ SHOOT
FLOWERS/ BUD
% FRUIT SET
BERRY WEIGHT
YIELD
.841**
.518*
.689*
−1.086**

Figure 7

IV. Discussion

There appears to be little compensation and covariation among life history traits in V. angustifolium. Each of the principal components had high coefficients and loadings for only one life history parameter, and only one negative relationship was observed among yield components in the path analysis. The patterns were highly plastic, but no strong associations were detected between demographic regimes and life history variation.

Several workers have proposed that the sequential development of components is adaptive because it allows investment to be regulated in response to immediate resource conditions (Lloyd 1980, Primack and Antonovics 1981). Pritts and Hancock (1985) postulated that independence among yield components between years may also be adaptive in perennial species. Our data on V. angustifolium are consistent with both hypotheses (Fig. 7, Table 7). There may have been little covariation because the initiation of flowering, vegetative bud break, fruiting, shoot elongation, inflorescence bud development and rhizome production in blueberries are usually separated by at least a two week period (Eck and Childers 1966). In addition, component values were generally uncorrelated between years. Since resource levels are not constant over time, each activity will respond to the current resource level. This would contribute to the absence of trade-offs in V. angustifolium, and supports the contention that temporally spaced development is selectively maintained.

The lack of covariation could also have occurred because each component was regulated principally by a distinct environmental parameter. Fruit set, which is associated with pollinator activity, was a major factor limiting sexual reproduction, while light availability had a positive effect on dry weight accumulation and inflorescence development (Fig. 6). Soil nutrient and water status were the major factors associated with clonal expansion and flowering (Fig. 6). Similar environmental-component correlations have been observed in other studies: moisture was associated with vegetative reproduction in Trientalis borealis (Anderson and Loucks 1973) and Solidago (Werner and Platt 1976); fertility affected vegetative reproduction but not sexual reproduction on Tussilago farfara (Ogden 1974); nitrogen had differential effects on growth and reproduction in several Vaccinium species (Ismail, et al. 1981, Chester and McGraw 1983); light intensity affected flowering but not vegetative reproduction in Fragaria (Dennis, et al. 1970); and pollination has been shown to limit sexual reproduction but not other life history parameters in several species (Salisbury 1942). Thompson and Stewart (1981), Abrahamson and Caswell (1982) and Watson (1984) have emphasized the need to identify limiting resources in studies of optimal partitioning.

Not all yield components in V. angustifolium were regulated by different environmental factors. Yield, berry number and berry weight were all strongly related to fruit set and, perhaps, pollination (Fig. 7). This was expected as a strong positive relationship between berry size and seed number, as determined by the number of fertilized ovules, has been reported in many studies of Vaccinium (Eaton 1967, Moor, et al. 1972, Darrow 1941). Flower bud number/shoot and flowers/bud were both strongly correlated with light availability. However, the overall interactions between components indicated independence ($W > 0.5$).

To determine if the component independence observed in V. angustifolium was unique, we examined data from published studies which measured intraspecific variation in three or more life history parameters (Table 9). It seems reasonable to assume that productivity, or size (BPS), is proportional to resource availability; therefore, this column was always considered positive. The direction of response in other variables was then related to size. Only five of 14 studies reported covariation among sexual reproductive effort, propagule size and number, and only one of these reported covariation in the direction predicted by life history theorists (McNamara and Quinn 1977). Similarly, there was no consistent trend showing a trade-off between vegetative and sexual reproduction. Unfortunately, data was available only on the direction of covariation, and not the rate of the various responses. The data would be more revealing if adjusted for size.

The absence of resource sharing has also been demonstrated with individuals, rather than populations. Bradbury and Hofstra (1977) found that individual leaves of Solidago canadensis do not export assimilate to inflorescences and

Table 9. Patterns of intraspecific covariation among life history traits and demographic parameters in various plant species. Components with the same sign covary in the same direction, opposite signs indicate negative covariation, and a '0' indicates no covariation. PN propagule number, PS propagule size, SRE sexual reproductive effort, VRE vegetative reproduction, BPS size or growth, DEN density, PFL percent flowering shoots.

Species	PN	PS	SRE	VRE	BPS	DEN	PFL
Amphicarpum purshii McNamara and Quinn (1977)	-	+	-		+		
Andropogon scoparius Roos and Quinn (1977)		+	+		+		
Arnica cordifolia Young (1983)	+	+	+	+	+	-	+
Aster acuminatus Pitelka, et al. (1980)			+	+	+	0	+
Aster acuminatus Winn and Pitelka (1981)			-	0	+	-	
Chamaenerion angustifolium van Andel and Vera (1977)	+	0	0		+		
Chamaesyce hirta Snell and Burch (1975)			+		+	-	
Chamaesyce hirta Snell (1976)	+	+			+	-	
Danthonia caespitosa Quinn and Hodgkinson (1984)	+	+	0				
Fragaria virginiana Holler and Abrahamson (1977)			0	+	+	-	
Heloniopsis orientalis Kawano and Masuda (1980)	+	-	-		+		
Impatiens capensis Abrahamson and Hershey (1977)	+		0		+		
Mimulus primuloides Douglas (1981)	+		0	+	+	-	
Plantago coronopus Waite and Hutchings (1982)	+	0	+		+	-	

Table 9. continued.

Species	PN	PS	SRE	VRE	BPS	DEN	PFL
Plantago lanceolata Primack and Antonovics (1981)	+	+			+		
Plantago lanceolata Primack and Antonovics (1982)			+	-	+		
Polygonum cascadense Hickman (1975)	+		-		+		
Rubus hispidus Abrahamson (1975b)			+	0	+		
Rubus trivalis Abrahamson (1975a)			0	+	+	-	
Rumex crispus Hume and Cavers (1983)	+	-	0		+		
Rumex crispus Weaver and Cavers (1980)	+		+		+		
Rumex obtusifolius Weaver and Cavers (1980)	+		+		+		
Senecio sylvaticus van Andel and Vera (1977)	+	+	0		+		
Senecio vulgaris Harper and Ogden (1970)			+		+	-	
Solidago canadensis Bradbury and Hofstra (1975)	0		0	0			
Solidago canadensis Werner (1979)	+	-	-	+			
Solidago sempervirens Cartica and Quinn (1982)	+	0	+		+		
Solidago pauciflosculosa Pritts and Hancock (1983b)	+	0	0		+	-	
Trifolium repens Turkington (1983)			-	+	+		-
Tussilago farfara Ogden (1974)	0	+	0	+	+	-	+

Table 9. continued.

Species	PN	PS	SRE	VRE	BPS	DEN	PFL
Tussilago farfara Bostock (1980)	+		+	0			
Typha latifolia Grace and Wetzel (1981)			−	+	+		+
Uvularia perfoliata Wigham (1974)	+		+	0	+	−	+
Vaccinium corymbosum Pritts and Hancock (1985a)	+	+	+		0		
Viola blanda Thompson and Beattie (1981)			0	0	+	−	+
Viola rostrata Thompson and Beattie (1981)			0	0	+	−	+
Viola soria Solbrig (1981)	+	+	0		+	−	

rhizomes simultaneously. Furthermore, the proportion of leaves exporting assimilate to rhizomes increased only after inflorescence development. In contrast, Hull (1969) demonstrated that simultaneous development of flowers and rhizomes occurs in Sorghum halepense, but sexual reproduction utilized only a small proportion of photosynthetic area. Finally, it must be emphasized that the patterns reported for V. angustifolium and other species are based on phenotypic responses to the environment. Genotypic differentiation could exist among these populations and influence the magnitude of the variation (Pritts, Hancock and Roueche 1985).

These findings have implications for several theories of life history evolution. For example, the prediction that woody plants have lower reproductive efforts than herbaceous species is based, in part, on the assumption of a trade-off between vegetative growth and reproduction (Mooney 1972). However, such a trade-off was not found in our study of V. angustifolium or previously in the woody plant species Solidago pauciflosculosa (Pritts and Hancock 1983a) and Vaccinium corymbosum (Pritts and Hancock 1985).

Abrahamson (1975b) predicted that vegetatived reproduction would be favored in low density habitats at the expense of sexual reproduction. While it may be true that fitness is increased by greater vegetative propagation, a decrease in sexual reproduction may not be necessary. Increased vegetative reproduction can be realized by an increase in plant size while allocation patterns remain constant (Winn and Pitelka 1981, Whigham 1974, Thompson and Beattie 1981).

Werner and Platt (1976) found an inverse relationship between seed size and number among species of Solidago, but did not find the same trend within a species. Even apparently strong relationships between taxons can disappear when adjusted for size (Stearns 1984). Trade-offs among components of growth and reproduction have not been conclusively demonstrated for a majority of plant species.

In conclusion, V. angustifolium populations exhibited wide variation for individual life history traits and there was considerable independence between traits. Yield components also behaved independently both within and between years. The presence of covariation among life history components is often assumed in theory and application. Data from V. angustifolium and other species suggest that this assumption may not be generally valid. Independence among components may have evolved as a means of maximizing reproductive output in variable environments.

CHAPTER FOUR - Identifying wild genotypes of *Vaccinium angustifolium* with high yield potential

I. Introduction

The germplasm base of cultivated highbush blueberries is quite narrow. In fact, most of the genes in 63 commercially released highbush cultivars originated from only 3 wild selections (Hancock and Siefker 1982). This situation has led to inbreeding depression, loss of genetic variation and limited adaptability (Hellman and Moore 1983, Lyrene 1983, Meader and Darrow 1947, Morrow 1943).

Two strategies have been employed to alleviate these problems. The first involves the introduction of genes from diploid and hexaploid species into the tetraploid gene pool (Ballington 1979, Darrow, et al. 1949, Draper 1977, Goldy and Lyrene 1984b, Moore 1965, Perry and Lyrene 1984). However, very few heteroploid pollinations result in viable progeny, only a small percentage of these progeny are true tetraploid hybrids and most of the are sterile (Goldy and Lyrene 1984a, Lyrene and Sherman 1983, Sharpe and Sherman 1971).

The second strategy involves the incorporation of wild germplasm from the same ploidy level into the cultivated gene pool (Darrow and Morrow 1952, Lyrene 1981, Lyrene and Sherman 1981). Homoploids are highly interfertile (Darrow and Camp 1945, Van der Kloet 1976b, Van der Kloet 1980, Van der Kloet 1983), but many wild plants are unproductive. A method is needed for selecting superior parents from the broad geographical range of blueberries.

Evolutionists have frequently described regular patterns of genetic differentiation among wild populations of individual species. If this has also occurred in native blueberry populations, a breeder might be able to locate superior genotypes by concentrating on environments in which horticulturally desirable traits have been naturally selected.

II. Methods

Seventeen diverse sites containing Vaccinium angustifolium populations were selected throughout Michigan (Table 4). Light levels were determined at each site during June of 1983 and expressed as the photosynthetic quantum flux density at the level of the blueberry foliage divided by the same density in full sunlight. Ten independnet measurements were made at mid-day at each site. Soil moisture levels were determined by randomly taking ten 5 cm^3 samples from the root zone of populations during a two week period in June, July and August of 1983. These samples were sealed in glass containers, weighed, oven-dried at 80C for one week and weighed again. Moisture level was expressed as the ratio of (wet weight - dry weight)/dry weight.

A minimum of 8 distinct clones were randomly selected from each site in March and April of 1983 while the plants were dormant. Individuals were excavated, transplanted into 20 cm pots containing equal amounts of peat and sand and placed in a greenhouse at East Lansing, Michigan. Flowers were removed during the 1983 growing season and the plants were allowed to go dormant in an unheated greenhouse during the late fall. In April of 1984, the average number of inflorescence buds per lateral shoot and the average number of flowers per bud were determined from 3 random samples from each genotype. All genotypes were pollinated every three days with a composite mixture of pollen using a camel hair brush. All ripened fruits were collected, oven-dried at 80C for one week and individually weighed. Specific leaf weights were also determined from a random sample of five leaves per plant.

Analysis of variance techniques for triply nested unbalanced designs were used to access the genetic variation in yield components. Coefficients for the estimated mean squares were calculated separately and used in the construction of F-tests (Anderson and Bancroft 1952). Correlation analysis was used to identify any association between performance in a common environment and characteristics of the original sites. A square-root arcsine transformation was applied to all percentage data to normalize the variances (Steel and Torrie 1980).

III. Results

Significant differences among locations (Southern Lower Peninsula, Northern Lower Peninsula, Upper Peninsula), populations within locations and genotypes within populations were detected for the number of inflorescence buds per shoot (Table 10). The differences among locations were associated with latitude as those from southern sites produced more buds than those from northern sites (7.34, 5.65 and 4.90 respectively).

Table 10. Analysis of variance for the number of inflorescence buds per lateral shoot, flower number per bud and individual fruit dry weight for genotypes of *Vaccinium angustifolium* in a common greenhouse environment.

Source of variation	d.f.	MS	EMS	F	p
BUDS PER SHOOT					
Locations	2	152.969	$\sigma^2 + 3.00\,\sigma_g^2 + 30.97\,\sigma_p^2 + 143.76\,\sigma_1^2$	4.557	0.01
Pop/Location	14	33.617	$\sigma^2 + 3.00\,\sigma_g^2 + 31.05\,\sigma_p^2$	1.691	0.05
Genotype/Pop	146	19.879	$\sigma^2 + 3.00\,\sigma_g^2$	9.390	0.001
Error	326	2.117	σ^2		
FLOWERS PER BUD					
Locations	2	75.406	$\sigma^2 + 3.00\,\sigma_g^2 + 28.31\,\sigma_p^2 + 125.42\,\sigma_1^2$	0.520	n.s.
Pop/Location	14	143.993	$\sigma^2 + 3.00\,\sigma_g^2 + 23.95\,\sigma_p^2$	18.540	0.001
Genotype/Pop	123	7.647	$\sigma^2 + 3.00\,\sigma_g^2$	2.936	0.001
Error	280	2.604	σ^2		
BERRY WEIGHT					
Locations	2	119.512	$\sigma^2 + 4.59\,\sigma_g^2 + 11.35\,\sigma_p^2 + 41.26\,\sigma_1^2$	1.650	n.s.
Pop/Location	13	57.415	$\sigma^2 + 3.12\,\sigma_g^2 + 10.27\,\sigma_p^2$	0.980	n.s.
Genotype/Pop	41	73.529	$\sigma^2 + 3.20\,\sigma_g^2$	2.640	0.001
Error	133	27.872	σ^2		

Also, genotypes sampled from low light environments produced significantly more inflorescence buds on average than those from high light environments ($r = -0.49$, $p < 0.05$) (Fig. 8).

The number of flowers per bud followed a similar trend. Significant differences existed among populations (Table 10), and these were negatively associated with light levels at the original sites ($r = -0.32$). However, a few outlying points (Fig. 9) prevented the relationship from being statistically significant ($p < 0.25$).

Significant differences existed among genotypes within populations for berry weight, but not among populations or locations (Table 10). However, berry size was significantly associated with moisture levels ($r = -0.57$, $p < 0.02$). Genotypes from drier sites produced larger berries on average than genotypes from mesic sites (Fig. 10).

IV. Discussion

The trends observed under common conditions were opposite to those observed under natural conditions (Pritts and Hancock 1985b). In the field, light availability was positively correlated with buds per shoot ($r = 0.608$, $p < 0.01$) and flowers per bud ($r = 0.490$, $p < 0.05$), while moisture level was positively correlated with berry size ($r = 0.332$, $p < 0.20$). This suggests that genotypes from resource limited sites are more efficient at sequestering resources for reproduction than genotypes from more optimal sites. Less efficient genotypes may have succumbed to competition and resource depletion as succession proceeded. The apparent efficiency exhibited by such genotypes

Figure 8.

Relationship between the production of inflorescence buds in a greenhouse environment and the light level at the site of origin for genotypes. Light level is expressed as the arcsine percent of photosynthetically active radiation measured as photon quantum flux density at the blueberry canopy, compared to measurements in full sunlight during late June, 1983.

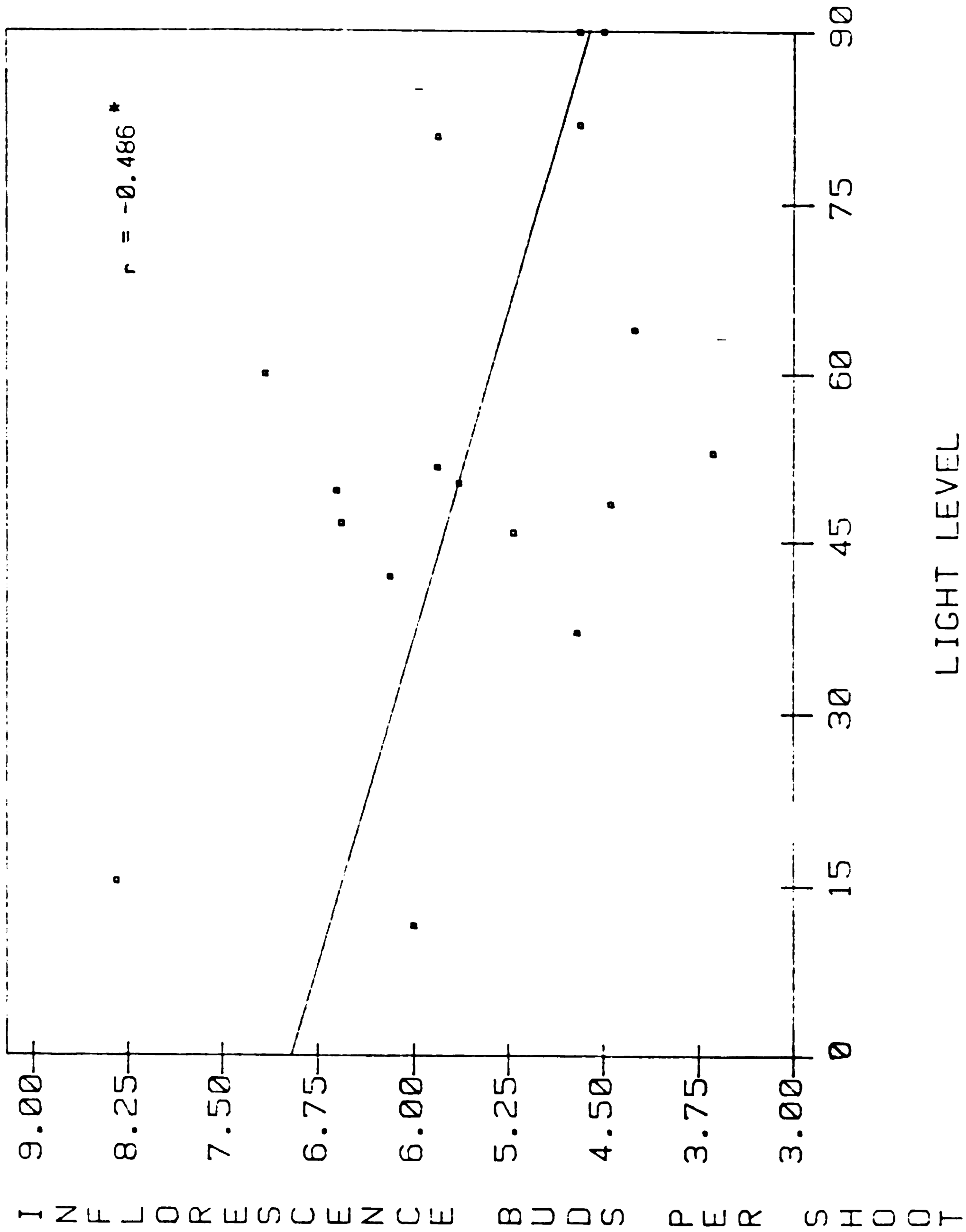

INFLORESCENCE BUDS PER SHOOT
9.00
8.25
7.50
6.75
6.00
5.25
4.50
3.75
3.00
0
15
30
45
60
75
90
r = -0.486*
LIGHT LEVEL

Figure 8

Figure 9.

Relationship between the production of flowers per bud in a greenhouse environment and the light level at the site of origin for the genotypes. Light level is expressed as the arcsine percent of photosynthetically active radiation measured as photon quantum flux density at the blueberry canopy, compared to measurements in full sunlight during late June, 1983.

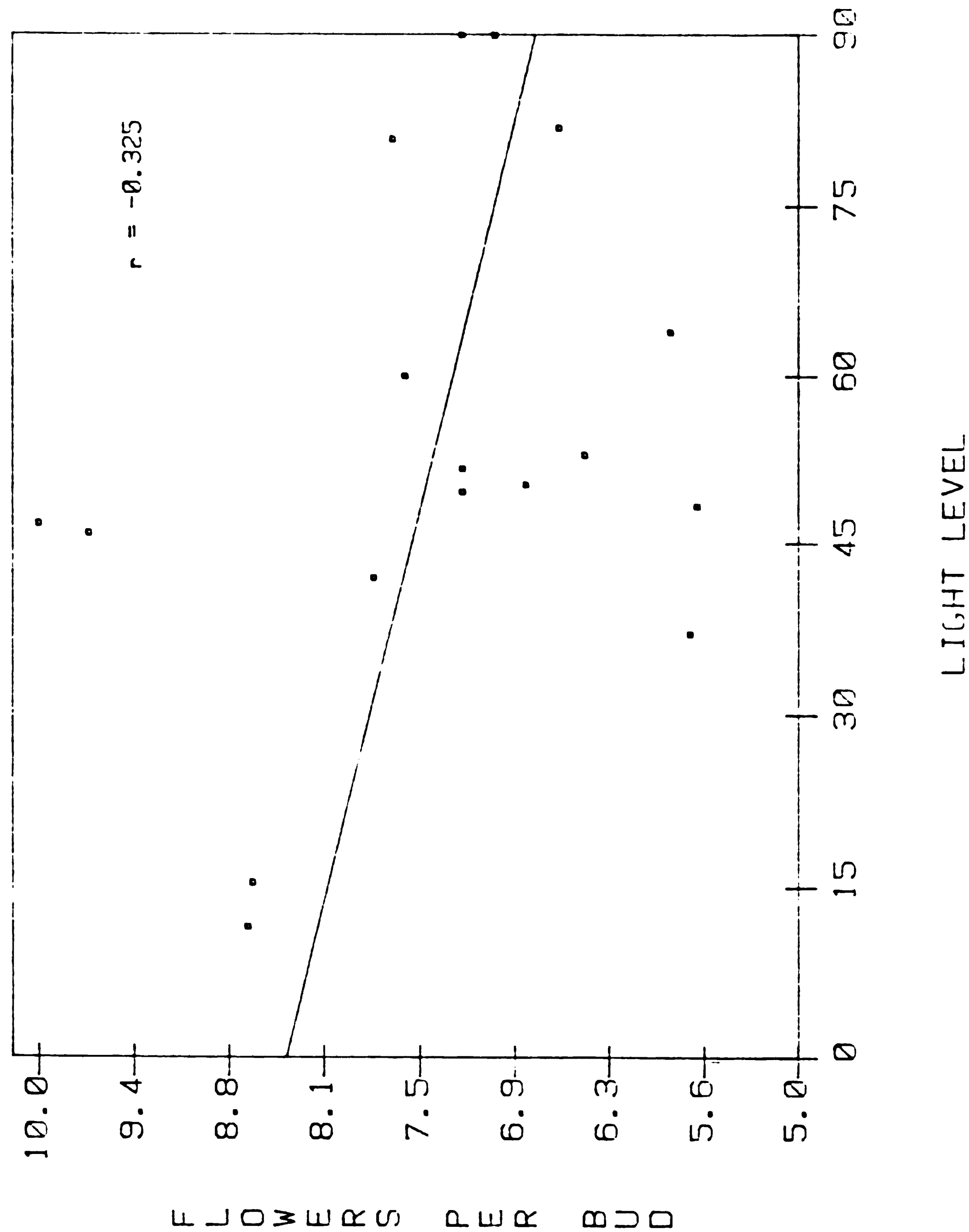

r = -0.325
FLOWERS PER BUD
10.0
9.4
8.8
8.1
7.5
6.9
6.3
5.6
5.0
0
15
30
45
60
75
90
LIGHT LEVEL

Figure 9

Figure 10.

Relationship between berry weight in a greenhouse environment and moisture level at the site of origin for the genotypes. Moisture level is expressed as the arcsine percent of gravimetrically determined water content in late June, 1983.

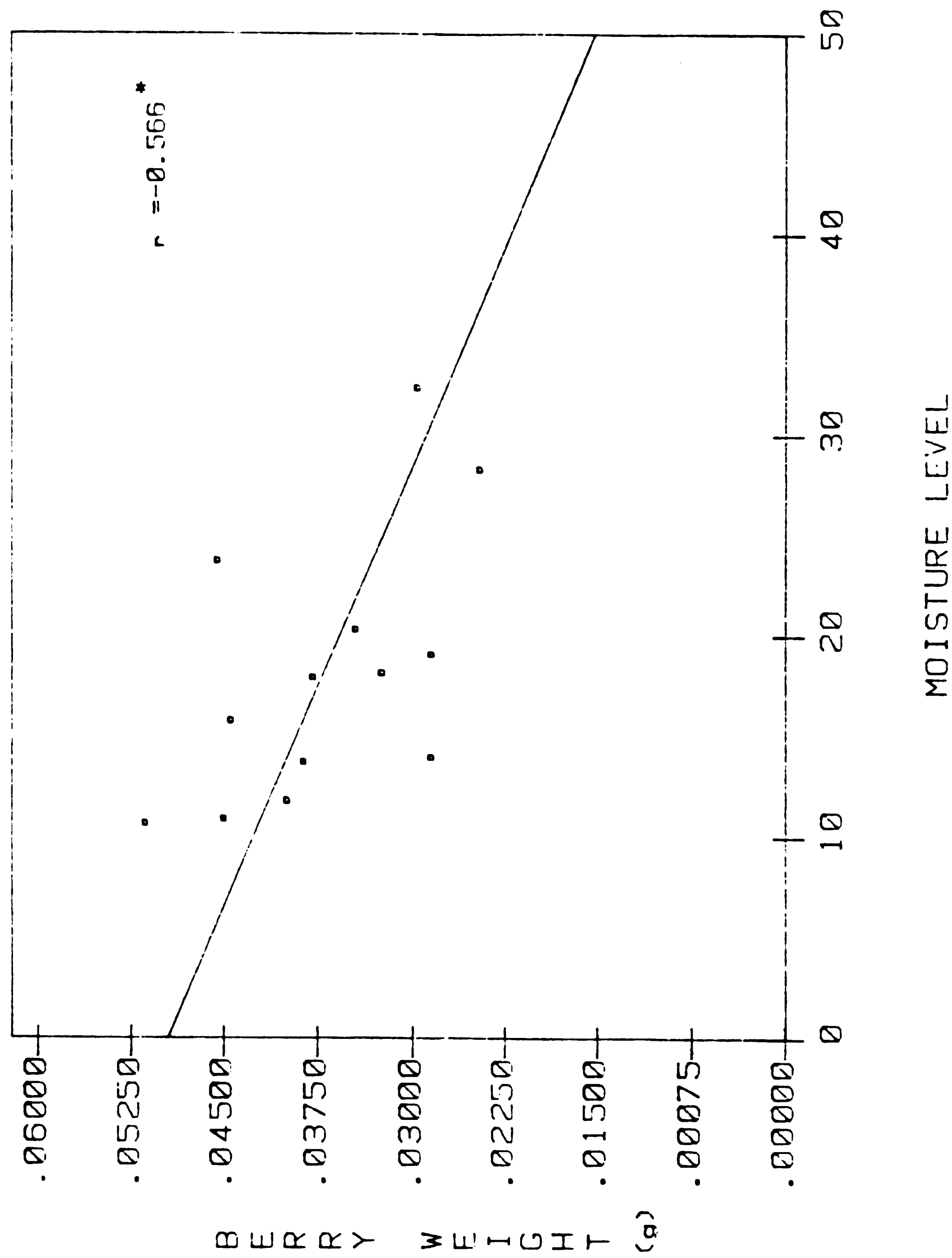

r =-0.566*
BERRY WEIGHT (g)
.06000
.05250
.04500
.03750
.03000
.02250
.01500
.00075
.00000
0
10
20
30
40
50
MOISTURE LEVEL

Figure 10

may be related to their inherent physiological plasticity, as plants from shaded sites exhibited higher specific leaf weights in the greenhouse than in the field (Fig. 11). Increased photosynthetic rates (Kappel and Flore 1983, Marini and Barden 1981, Pearce, et al. 1969) and water use efficiencies (Nobel 1980) have been associated with specific leaf weight.

Thus, natural environments exist in Michigan which are more likely than others to contain horticulturally desirable genotypes. There is substantial inter-populational variability, but a breeder still has a greater probability of selecting a genotype with a high yield potential from a southern, dry, shaded site than from a northern, moist, sunny one. It is not known how these plants will perform under cultivated conditions, but our greenhouse conditions probably relate more closely to a producer's field than the natural environment.

Figure 11.

Relationship between light level and specific leaf weights of genotypes from 17 sites as determined in the field and the following season in a common greenhouse environment. Light level is expressed as the arcsine percent of photosynthetically active radiation measured as photon quantum flux density at the blueberry canopy, compared to measurements in full sunlight during late June, 1983. Solid lines and (•) represent the response measured in the field prior to transplantation. Broken line and (X) represent the response measured in a common environment after transplantation.

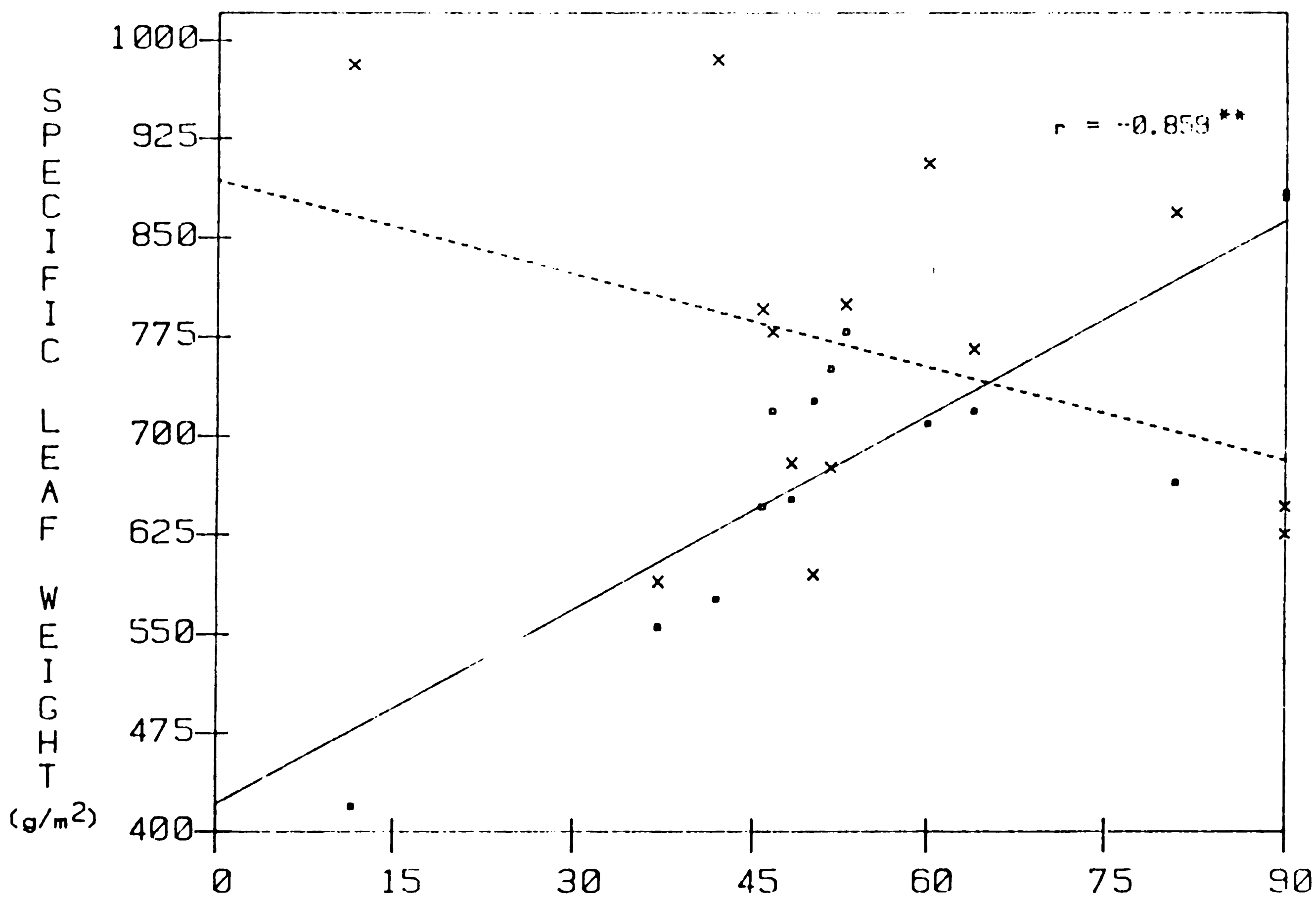

r = -0.859**
SPECIFIC LEAF WEIGHT (g/m2)
1000
925
850
775
700
625
550
475
400
0
15
30
45
60
75
90
LIGHT LEVEL

Figure 11

CONCLUSIONS

Powerful methods have been developed to quantify relationships between environment and growth parameters, and to analyze interactions among components of complex traits. These methods were used to analyze relationships among environmental, life historical and yield components in wild populations of Vaccinium corymbosum and V. angustifolium in Michigan. The most striking observation was the independence exhibited by life history and yield components over a two year period for both species. This lack of covariation could partially be attributed to component regulation by different, independent environmental factors. Furthermore, components of life history and yield develop sequentially and would likely not simultaneously share resources. Any fluctuation in resource level during the period of active growth and development would also contribute to the lack of covariation among components.

Uncoupling the response of fitness components may be advantageous to plants encountering variable environments. Such plants could regulate investment in several stages in response to immediate resource conditions. Commitments made in a series of steps should be less vulnerable to environmental variation than those made at a single period of time or those fixed genetically. The sequential development of components has been reported for many other plant species, and may be selectively maintained in individuals encountering unpredictable resource levels over short periods of time.

The lack of covariation observed in Vaccinium has implications for life history theory. Most theories assume trade-offs occur among life history components, but none were found between fruit size and number, vegetative and sexual reproductive effort or reproductive and vegetative growth. Independence among these parameters was also common in many other species. It appears that predictions based on assumptions of trade-offs should be revised.

The independent nature of life history and yield components has horticultural implications as well. This study suggests that yield improvement can be achieved through the manipulation of different components at several times through the year. Because of their independent nature, changes in one component will generally not affect the response of another. As a result, an increase in specific environmental factors may be necessary only at certain critical times. Maintenance of high levels of resources throughout the entire year may involve unnecessary expenditures. In addition, the decreasing efficiency of fruit production associated with the age of canes suggests that pruning is necessary to maintain vigor and productivity.

Yield components can also be manipulated genetically. In fact, genetically-based differences in life history components exist in nature and are associated with measurable environmental variables. These differences can be exploited by breeders seeking specific combinations of characters difficult to obtain under artifical conditions. Specifically, the number of inflorescence buds on a shoot had the greatest effect on yield in both species when the effect of size was removed. Although this study suggests that tremendous potential exists for blueberry improvement, the efficacy of using wild germplasm must now be accessed under more controlled conditions.

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