GROWTH AND YIELD RELATIONS
IN
HIGHBUSH BLUEBERRY

BY

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ABSTRACT

It was proposed that sequential yield component analysis could determine some growth and yield relations in highbush blueberry which could not be detected by ordinary regression procedures. The technique was applied to a commercial planting of the cultivar 'Bluecrop' in Pitt Meadows, British Columbia. Yield per bush depended most upon yields of individual canes. Ripe berry yield per cane was determined either by fruit set or the number of seeds per berry. Fruit set and berry enlargement determined green fruit yield per cane and ripening was related to bush canopy area. Buds initiated and the portion which differentiated into reproductive buds determined yield of clusters per cane. Cane thinning had beneficial effects upon growth and development while top thinning seemed to limit growth. No biennial bearing tendencies could be detected. It was concluded that sequential yield component analysis is a valuable technique for studying plant growth and yield relations, but interpretation problems can result if modelling assumptions are not met.

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B - total number of berries

Bd1 - number of buds initiated in 1980

Bd2 - number of buds initiated in 1981

BH1 - number of first harvest berries

BH2 - number of second harvest berries

BH3 - number of third harvest berries

Br - number of branches

Bu - bush

Ca - number of canes

CaN - number of canes emerging in 1981

Cl1 - number of flower clusters, 1981

Cl2 - number of flower clusters, 1982

Cp - canopy area (cm^2)

Cr - crown area (cm^2)

D - cane diameter (mm)

GB - number of green berries

F - number of flowers

GBW - green berry weight (g)

Ht - cane height (cm)

Ln - total branch length per cane

R^2 - coefficient of determination

RB - number of ripe berries from all harvests

RBH1 - number of first harvest ripe berries

RBH2 - number of second harvest ripe berries

RBH3 - number of third harvest ripe berries

RBW - ripe berry weight (g) from all harvests

RBWH1 - first harvest ripe berry weight (g)

RBWH2 - second harvest ripe berry weight (g)

RBWH3 - third harvest ripe berry weight (g)

S - total number of seeds

SD - number of developed seeds

SDH1 - number of first harvest developed seeds

SDH2 - number of second harvest developed seeds

SDH3 - number of third harvest developed seeds

SH1 - total number of first harvest seeds

Sh1 - number of vegetative shoots, 1981

Sh2 - number of vegetative shoots, 1982

SH2 - total number of second harvest seeds

SH3 - total number of third harvest seeds

SPGA - sequential plant growth analysis

SU - number of undeveloped seeds

SUH1 - number of first harvest undeveloped seeds

SUH2 - number of second harvest undeveloped seeds

SUH3 - number of third harvest undeveloped seeds

SYCA - sequential yield component analysis

YCA - yield component analysis

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1. INTRODUCTION

Two schools of thought have dominated research into the origins of crop yield. Workers of both schools have devised and used various methods of analysis but many of these extract less information than what may be desired or even available from collected data.

One school deals with attributing plant or crop yield variability to that of morphological components known as yield components. The most commonly used yield component analyses were recently reviewed by Fraser and Eaton (1983) and regression or correlation procedures were common to all of them. Multicollinearity, which is common among yield components, is often ignored or dealt with by grouping collinear components. However, in an analysis introduced by Eaton and Kyte (1978), multicollinearity is considered to result from components affecting later components during development. This analysis has since been supplemented and was named sequential yield component analysis (SYCA). In SYCA a model based on the assumed developmental sequence of components is used to separate and calculate independent component contributions to yield variability.

The other school has concentrated on the economics of assimilate partitioning and various meaningful indices have been derived which indicate efficiency in partitioning. Analyses formulated by this group include traditional plant growth analysis, as reviewed by Hunt (1978), and demographic analysis which was first described by Bazzaz and Harper (1976). Researchers who employ these techniques may be interested in total dry matter yield or a portion which is utilized agronomically. Hunt (1978) described several of the growth indices which are computed in traditional plant growth analysis. Statistically sound comparisons are made between indices obtained within correctly designed experiments, but these tell little about the origins of total or harvestable yield variability. Jolliffe et al. (1982) recently addressed this problem and outlined a technique which includes traditional growth analysis indices as components of yield in a SYCA. The analysis, named sequential plant growth analysis (SPGA), determines the relative contribution of growth indices to final yield variability.

SYCA and SPGA results may be as complicated as the plants they are obtained from. Results and interpretation of SPGA have not yet been reported but SYCA has been applied to a number of crops and interpretations of various result-combinations have been published. A clear guide to interpretation of these sequential analyses is lacking and would require a thorough review of the work done to date and perhaps further studies using more complicated models.

A few reported correlations between aspects of growth and yield in blueberry provide only a sketchy picture of

how yield is determined by its components and their interrelations. This thesis was undertaken to show that SYCA can supply much of the information needed for a more complete picture since the shrub habit of blueberry provides several bases for developmental modelling. Six SYCA models are proposed and examined, new SYCA result-combinations are interpreted and the shortfalls and potential uses of SYCA are discussed.

2. LITERATURE REVIEW

2.1. Growth habit

The highbush blueberry, *Vaccinium corymbosum* L., is a 2 to 3 meter high crown-forming shrub. It has 2 to 5 canes from single boles, and occasionally suckers when disturbed or burnt (Van der Kloet, 1980). Cultivated varieties are held back to a height of 6 to 8 feet by pruning (Cain and Eck, 1966). Most varieties branch readily from the crown and sometimes send up suckers from the roots several inches away thus forming a bush with several stems or canes arising from the ground level (Cain and Eck, 1966).

Details of vegetative development have been described (Gough et al., 1978a). In the spring vegetative buds begin developing into shoots which extend at various rates during the growing season. Throughout the season a varying number of apical abortions occur after which a distal subtending bud develops and assumes apical dominance. Shoots often remain unbranched although branching is not rare. Final shoot thickness and length vary within a bush.

Flower bud initation follows cessation of vegetative growth (Gough et al., 1978b). This stage was detected on August 21 in 1975 and in early August in 1976 for 'Bluecrop' (Gough et al.,1978b). Flower bud development was observed to continue until the begining of December and then remain arrested until mid-March (Gough et al., 1978b).

On any flush most distal buds are reproductive while proximal buds are usually vegetative (Gough et al., 1976). Reproductive buds develop into racemes or clusters of 5 to 10 flowers (Cain and Eck, 1966). Fruit development in blueberry is of the 3 stage type similar to peach, cherry and fig and the duration of stages II and III determine the duration of development (Young, 1951).

Blueberries contain both large and small seeds (White and Clark 1938; Bell 1957). Seeds of two sizes from *Vaccinium angustifolium* Ait., a species closely related to *Vaccinium corymbosum* L., have been described (Bell, 1957). Small seeds were observed to be abnormally developed ovules without embryos while large seeds were conspicuously pitted and contained embryos, many of which had died at some stage of development. Large seeds were always clustered around the top of the central axis, and small seeds at the lower and basal portion of the loculi. It was suggested that there had been insufficient pollen tubes to fertilize all of the ovules.

2.2 Growth and yield relations

2.2.1 Shoot thickness and length

Thin shoots of highbush blueberry were found to have smaller and fewer xylem vessels than thick shoots and it was estimated that thick shoots could have 10 to 25 times the conductive capacity of thin shoots (Shutak et al., 1957). Shoot thickness was positively related to yield of reproductive buds and inversely related to yield of winter damaged shoot tips in a study of mowed bushes during regrowth (Bowen and Eaton, 1983). Long thick laterals have been observed to have a greater ratio of vegetative shoots to fruiting clusters and a greater portion of blossoms becoming berries, than short thin laterals (Filmer and Marucci, 1963). Multiple reproductive buds were found to occur more often on thick shoots than on thin or medium-thick shoots (Gough et al., 1976), but development of reproductive buds was observed to be slower on thick shoots (Shutak et al., 1957). Flowers borne on thick shoots were reported to bloom later and develop into larger less variable fruits (Hindle et al., 1957a; Shutak et al., 1957). No relation was detected between wood thickness and days to fruit maturity (Hindle et al., 1957b; Shutak et al., 1957).

2.2.2 Blossoming and fruit development

Results of a blueberry maturity study found that the time from first bloom to first harvest is too variable to be used in estimating harvest dates (Meader and Darrow, 1947). Fruit maturity seems unrelated to position within a cluster, but late blossoming clusters have been observed to mature fruit over a shorter than average time range (Young, 1951). Fruit size was found to decrease with progressively later harvests (Moore et al., 1972).

2.2.3 Seeds

It has been suggested that hormones are activated by fertilization in species closely related to *Vaccinium corymbosum* Ait. and large amounts of hormones which stimulate fruit enlargement are released even before abortion occurs (Meader and Darrow, 1944). An early study found no relation between seed number and berry size in highbush blueberry (Merrill, 1936). Reports from other early studies imply a relation but present no statistical evidence (Bell, 1957; Darrow, 1958; Meader and Darrow, 1944; White and Clark,1938). Significant correlations between developed seed number and weight of individual berries were found in 10 out of 14 cultivars included in one study (Eaton, 1967). Coefficients of determination ranged from 10% to 39% and regression coefficients ranged from 5.4 to 14.7 mg/seed. Cultivar mean berry weight was also related to mean seed number with a regression coefficient of 21.5 mg/seed. Another study found that cultivar mean berry weight correlated better with mean developed seed number than with mean total seed number (Moore et al., 1972). This study also found other relations between seed number and fruit development including a positive correlation between mean berry weight and the percent of seeds developed and a negative correlation between the number of developed seeds per fruit and fruit weight per developed seed.

Seed counts from several highbush cultivars have been reported (Darrow, 1958; Eaton, 1967; Moore et al., 1972). One study found a range in cultivar mean counts of 15.7 for 'Brooks' to 73.8 for 'Ivanhoe' (Darrow, 1958). Mean counts reported for 'Bluecrop' have been 63 (Darrow, 1958), 47 (Eaton,1967) and 46 (Moore et al., 1972). Seed number has been found to decrease with later harvests (Darrow, 1958; Moore et al., 1972).

Cross pollination was found to enhance fruit size (Morrow, 1943; Eaton, 1967), fruit set and early ripening (Morrow, 1943). In a pollination study, seed weight was found to depend on the female parent and not on the male (Morrow, 1943).

2.3 External influences on growth and yield

2.3.1 Shading

Clusters exposed to sunlight have been observed to mature earlier (Hindle et al., 1957a; Young, 1951) and produce larger fruit (Young, 1951) than those in the shade. A reduction in early ripening was obtained by bagging clusters with light-proof bags (Shutak et al., 1956).

2.3.2 Nutrients and water

Nitrogen was reported to be the most important element for normal growth of young highbush blueberry plants (Kramer, 1942). Withholding nitrogen from young plants was found to induce apical abortions which were associated with a reduction plant top weight.

In general blueberries can perform normally with a considerably lower nutrient supply than that needed by other deciduous fruits (Cain and Eck, 1966). Deficiencies in any of the macronutrients result in reduced growth. Nutrients whose deficiencies cause distinct visible changes in growth are boron and zinc, which result in shortened internodes near the tips of shoots, and phosphorus and nitrogen, which result in reduced shoot growth and small young leaves (Cain and Eck, 1966). Fruit size was found to suffer during years of extreme drought (Young, 1951).

2.3.3 Pruning and thinning

Several government extension bulletins on blueberry growing (Bell and Johnson,1962; Darrow, 1951; Johnson, 1959; Thorpe, 1971; Dodge, 1969) describe similar pruning methods for blueberries. Reasons for pruning include promotion of earlier ripening, enhancement of fruit size and induction of new cane emergence. It is recommended that wood removed during pruning include dead or injured branches, fruiting wood close to the ground, shoots and canes of low vigor as well as short soft late developing shoots. Less pruning is recommended for vigorous cultivars but enough wood should be removed for good light penetration.

Very heavy pruning was observed to reduce yield from 'Rubel' bushes by 75% the first year and 50% the second year compared with light pruning, while berry size was increased by 25% the first year and 30% the second year (Darrow, 1951). Cluster thinning after fruit set was found to reduce total yield per bush, increase berry size, and advance peak harvest time (Ballinger et al., 1963).

2.3.4 Growth regulators

Several auxins and a gibberellin, KGA_3, were found to induce fruit set and parthenocarpic fruit development in highbush blueberry while kinetin, maleic hydrazide and daminozide had no effect (Mainland and Eck, 1968a). A combination of KGA_3 and an auxin, NAA, was more effective at inducing fruit set than either growth regulator used alone and fruit from flowers treated with high concentrations of KGA_3 and NAA together ripened earlier than pollinated fruit (Mainland

and Eck, 1968b). KGA_3 also enhanced fruit enlargement and treated berries had growth rates which were greater in the initial swell and less in the final swell than pollinated berries. GA_3 applied to blueberry flowers for two consecutive years increased fruit set in the first year but not in the second, while yield increased in the second year and was unaffected in the first (Mainland and Eck, 1969). The number of reproductive buds initiated in either year was unaffected by GA_3 treatments. Fruit from flowers treated with GA_3 has been compared to fruit from control flowers which had not been exposed to bees (Hooks and Kenworthy, 1971). GA_3 increased fruit size and yield per bush and reduced seed weight per fruit. It was suggested that GA_3 substituted for the effect of pollination and fertilization.

Daminozide, applied at 5000 ppm to blueberry bushes on July 31 one year after mowing, increased the average number of flowers buds per 5 inches of growth from 1.3 to 4.2 on the whole shoot, and from 3.5 to 7.9 on the second flush (Shutak, 1968). Multiple reproductive buds were also observed on treated plants. Daminozide, applied at 5000 ppm to 'Colins' and 'Bluecrop' on either or both of July 18 and August 22, retarded shoot elongation and its effect was most pronounced with 2 sprays (Hapitan et al., 1969). The number of reproductive buds per shoot length was increased by the treatments but blossoming and fruit ripening were delayed in the following year. Spray date did not affect reproductive bud counts but bushes sprayed in July or on both dates had more flowers in the third and fourth clusters than controls. A treatment X cultivar interaction indicated differential cultivar response. Shoot abortion pattern was not altered by daminozide when it was applied at 5000 ppm one month after bloom for 2 years (Gough et al., 1978a and 1978b). Shoot growth was substantially reduced in pruned bushes but not in those left unpruned for 2 years. Although bloom was delayed by about 2 weeks in the following year, bud development was similar to control plants.

Daminozide has been described as an antimetabolite which probably acts by reducing the amount of gibberellin synthesized by the plant (Cathey, 1964). Gibberellins are involved in the cell expansion phase of fruit development but are available in supraoptimal amounts so that although essential for development they are unlikely to become limiting (Luckwill, 1979). Effects of daminozide upon fruit development in highbush blueberry have not been reported. Daminozide applied during fruit ripening of the lowbush blueberry, *Vaccinium angustifolium* Ait., had no effect on the rate of ripening (Ismail, 1974). When applied to cranberry, *Vaccinium macrocarpon* Ait., 2 weeks before harvest, daminozide was found to have no effect upon yield or berry size during 3 years of testing (Eck, 1972).

Ethephon applied to highbush blueberries 2 weeks before the first harvest was found to increase the percentage of total yield in the first harvest (Eck, 1970). The concentration required for response differed among cultivars and ethephon-treated berries were smaller than controls.

2.4 Sequential yield component analysis

Sequential yield component analysis (SYCA) was first employed in a cranberry study (Eaton and Kyte, 1978). Potential components were included in multiple regressions sequentially in the assumed order of development and the increment in R^2 was calculated at each step.
Not only was yield predicted by its components but components were also predicted by earlier components. This enabled component compensation and the degree of environmental influence to be detected. This method has also been applied to studies of white clover (Huxley et al., 1979), bean (Herath and Eaton, 1981) and again to cranberry (Yas and Eaton, 1981; Shawa et al., 1981). The technique was developed further in a highbush blueberry study (Bowen and Eaton, 1983). In this, components were included in multiple regressions in the reverse to

developmental order and R^2 increments were calculated. This analysis is called backward SYCA and the original analysis is called forward SYCA. The order of inclusion of the yield components into the regressions determines the meaning of the R^2 increments. A component might affect yield directly, or indirectly by contributing variability to later components which in turn affect yield. R^2 increments from a forward SYCA measure the combined direct and indirect effects of components after all effects of developmentally earlier components have been considered. R^2 increments from a backward SYCA measure direct effects of components including effects of earlier components which are affecting yield through the component measured. Component mode of action is determined from differences between results of forward and backward analyses (Bowen and Eaton, 1983). This method has been applied to cranberry (Eaton, Shawa and Bowen, 1983), pea (Anderson et al., 1983), bean (Lovett Doust et al., 1983) and cucumber (Bowen, 1983).

3. MATERIALS AND METHODS

3.1 Experimental design

Treatments were chosen that were considered to have potential to affect growth. These consisted of factorial combinations of cane thinning and canopy or top thinning, both with unpruned controls, and daminozide (B-Nine, Uniroyal) sprays with concentrations of the active ingredient, butanedioic acid mono-(2,2-dimethyl hydrazine), at 0, 5000, and 10,000 ppm on a weight per volume basis. The 12 treatments were replicated once and applied at random to 24 'Bluecrop' bushes in a commercial planting at Pitt Meadows, British Columbia.

3.2 Treatment application

Cane thinning was applied before canopy thinning on February 2, 1981. daminozide was applied on August 4, 1981 with the 0 concentration applied as water.

3.3 Yield component models

Models proposed for yields of ripe fruit, green fruit and clusters are presented (Table 1). These models express yield in terms of its potential components. Two models were proposed for each type of yield to reduce the number of components per analysis. Models Ia, IIa and IIIa subdivided yield variability among bushes; the data required are means per bush. Models Ib, IIb and IIIb subdivide yield variability among canes; the data required are values from individual canes. All variability in yield is accounted for by variation in its components. The primary data required from each bush to calculate ratios in the models were crown area (Cr), cane number (Ca), and yields of ripe berries (RBW), green berries (GBW) and flower buds (Cl2). Data required from each cane were height (Ht), branch number (Br), total branch length (Ln), shoot number (Sh1), cluster number (Cl1), flower number (F), ripe berry number (RB), total seed number (S), developed seed number (SD), ripe berry weight (RBW), green berry number (GB), green berry weight (GBW), number of buds initiated (Bd2) and the number of reproductive buds which produced clusters in the following year (Cl2). Other variables of interest but not included in the models were the number of new canes which emerged (CaN), canopy area (Cp) and, from each harvest, berry number (BH1, BH2, BH3), berry weight (RBWH1, RBWH2, RBWH3), undeveloped seed number (SUH1, SUH2, SUH3) and developed seed number (SDH1, SDH2, SDH3).

3.4 Data collection

3.4.1 Dates of harvests and data collection in the field

Table 1. Sequential yield component models.

MODEL Ia Ripe fruit yield per bush

$$\frac{Cr}{Bu} \times \frac{Ca}{Cr} \times \frac{RBW}{Ca} = \frac{RBW}{Bu}$$

MODEL Ib Ripe fruit yield per cane

$$\frac{D}{Ca} \times \frac{Ht}{D} \times \frac{Br}{Ht} \times \frac{Ln}{Br} \times \frac{Bd1}{Ln} \times \frac{Cl1}{Bd1} \times \frac{F}{Cl1} \times \frac{B}{F} \times \frac{RB}{B} \times \frac{S}{RB} \times \frac{SD}{S} \times \frac{RBW}{SD} = \frac{RBW}{Ca}$$

MODEL IIa Green fruit yield per bush

$$\frac{Cr}{Bu} \times \frac{Ca}{Cr} \times \frac{GBW}{Ca} = \frac{GBW}{Bu}$$

MODEL IIb Green fruit yield per cane

$$\frac{D}{Ca} \times \frac{Ht}{D} \times \frac{Br}{Ht} \times \frac{Ln}{Br} \times \frac{Bd1}{Ln} \times \frac{Cl1}{Bd1} \times \frac{F}{Cl1} \times \frac{B}{F} \times \frac{GB}{B} \times \frac{GBW}{GB} = \frac{GBW}{Ca}$$

MODEL IIIa Cluster yield per bush in 1982

$$\frac{Cr}{Bu} \times \frac{Ca}{Cr} \times \frac{Cl2}{Ca} = \frac{Cl2}{Bu}$$

MODEL IIIb Cluster yield per cane in 1982

$$\frac{D}{Ca} \times \frac{Ht}{D} \times \frac{Br}{Ht} \times \frac{Ln}{Br} \times \frac{Bd1}{Ln} \times \frac{Sh1}{Bd1} \times \frac{Bd2}{Sh1} \times \frac{Cl2}{Bd2} = \frac{Cl2}{Ca}$$

Notation as in List of Symbols

Ten canes per bush were chosen at random and tagged on February 2, 1981. All data collected on a per cane basis were taken from tagged canes. Clusters and flowers were counted during May 15 and 16, 1981. Measurements of cane height (cm), cane diameter (mm), and the number and length (cm) of branches were taken during June 24 to July 3, 1981. Ripe berries were harvested on July 31, August 6, and August 21, 1981. On August 26, 1981 newly emerged and other canes were counted separately and measurements of canopy perimeter (cm) and crown perimeter (cm) were taken. Clusters and shoots were counted on May 4, 1982.

3.4.2 Fruit and seed data

Fruit from each cane was frozen in a plastic bag on the day it was harvested. Berries from each sample were counted and weighed (g) and ten berries were sampled at random for seed counts. Seed extraction was similar to that described in a previous study (Morrow et al., 1954) but modifications prevented loss and damage. Berries in each sample were frozen and dipped in hot water so that the skins slipped off easily. peeled berries were then added to 200 ml of water in a 250 ml blender jar and procesed on "stir" for about 5 seconds with an 'Osterizer' blender equipped with a dull blade. After the seeds settled to the bottom of the jar the remaining suspended pulp was carefully decanted and discarded. Water was added to the jar and if pulp settled with the seeds they were stirred manually and the liquid decanted a second time. Seeds were drawn into a 7 ml polyethylene transfer pipette and transferred onto a ceramic spot plate to dry.

Seeds were either large and brown or small and yellow (Figure 1). Counted samples of both seed types ranging from 20 to 200 in multiples of 20 were obtained to determine the mean projected area of each type by using a leaf area meter. A film of mineral oil between 2 pieces of Saran Wrap was not traceable by a Li-Cor LI-3000 leaf area meter. The counted seeds were mounted between 2 Saran Wrap sheets spread with a thin film of mineral oil. A dessert spoon was then used to gather and spread the seeds in a single layer at the centre of each mount so that they touched but did not stack. The mineral oil held the seeds in place. Three replicate readings were made on each mount with the leaf area meter, making 60 readings which were taken in a random sequence for each type. Coefficients of linear regression of meter reading upon seed count provided the mean projected area of each seed type. The mean projected area of a large seed was 1.207 $\pm$ 0.019 mm^2 and the R^2 from the regression was 99%. Small seeds had a mean projected area of 0.435 $\pm$ 0.015 mm^2 and the R^2 from the regression was 96%. All seed samples were mounted in the manner described and area readings were taken. Each mount

Figure 1. Two seed types extracted from ripe 'Bluecrop' berries (x 20)

was then placed under a dissecting microscope and seeds of both sizes were counted within the 65 mm^2 field of view. Seed number estimates were calculated from derived equations (Table 2).

3.5 Statistical analyses

3.5.1 Treatment effects upon component means

Components and component ratios were calculated on per bush and per cane bases. Data were estimated for each bush when measurements were made only on a per cane basis by multiplying cane number by the amount per cane. Analysis of variance was used to detect differences due to treatment for each component and component ratio.

3.5.2 Yield component analyses

SYCA was carried out as described in earlier studies (Bowen and Eaton, 1983; Lovett Doust et al., 1983; Bowen 1983). Components and yield were predicted by developmentally earlier components. Variables were included sequentially in multiple regressions and the increment in R^2 was calculated at each step. In the forward analysis of yield, the order of inclusion of the independent variables was the assumed developmental order shown in the models (Table 1). In the backward

Table 2. Equations for estimating seed counts.

$$M = \frac{PL}{a} \qquad (1)$$

$$P = \frac{ma}{ma + nb} \qquad (2)$$

Substituting (2) into (1):

$$M = \frac{mL}{ma + nb} \qquad (3)$$

$$N = \frac{QL}{b} \qquad (4)$$

$$Q = \frac{nb}{ma + nb} \qquad (5)$$

Substituting (5) into (4):

$$N = \frac{nL}{ma + nb} \qquad (6)$$

---

a - estimated area of a large seed (1.207 mm^2/seed)
b - estimated area of a small seed (0.435 mm^2/seed)
L - area of mixed seed in a sample (mm^2)
M - number of large seeds in the sample
m - number of large seeds counted in 65 mm^2 of the sample
N - number of small seeds in the sample
n - number of small seeds counted in 65 mm^2 of the sample
P - portion of the sample area containing large seeds
Q - portion of the sample area containing small seeds

analysis the order of inclusion was reversed but the yield and independent variables were the same.

3.5.3 Treatment effects upon component contributions to yield

SYCA was applied to data of each pruning treatment level. R^2's obtained were compared by applying a Z test (Zar, 1974).

3.5.4 Harvest trends

Analysis of variance was used to detect harvest trends in yields and fruiting properties. This analysis procedure also enabled interactions between harvest and treatments to be tested.

3.5.5 Biennial bearing tendencies

SYCA was used to detect biennial bearing tendencies by expressing cluster yield in 1982 in terms the flowering and fruiting components of 1981.

3.5.6 Canopy area

Canopy area did not fit into the developmental sequence of any of the models. Since it had potential to affect yield or components throughout the growing season, each bush component was regressed individually upon canopy area to determine the effects of bush spread upon growth and yield.

3.5.7 New cane emergence

Each bush component had potential to affect or be affected by the number of new canes which emerged. New cane number was regressed upon each bush component to determine the relations between bush structure and new cane emergence.

4. RESULTS AND DISCUSSION

4.1 Treatment effects upon cane components

Means and standard deviations of cane components (Table 3) describe some statistical properties of the variables considered in this study. These statistics provide a useful reference since SYCA deals only with variability.

Cane thinning resulted in a lesser mean for cane height (Ht) and a greater mean for branches per height (Br/Ht) (Table 4). This indicates that the pruning treatment was effective in removing tall spindly canes. The portion of buds which differentiated into clusters (Cl2/Bd2) and cluster yield per cane (Cl2/Ca) were promoted by cane thinning. It is possible that these beneficial effects resulted from better light penetration to leaves which increased photosynthesis and perhaps the carbon to nitrogen ratio.

Desired reductions in branch number (Br) and total branch length (Ln) were provided by top thinning (Table 4). In response, fruit set (B/F) and total seeds per berry (S/B) were reduced. Since wood which bore vegetative buds was removed, it is possible that the loss of potential shoots and leaf area allowed fewer berries and seeds to set. Undeveloped seed number in the first harvest (SUH1) was reduced by top thinning but the number of developed seeds (SDH1) was not affected (Table 4). Top thinning was

Table 3. Means and standard deviations of cane components.

	Means	Standard Deviations
B	197.	151.
Bd1/Ln	0.33	0.24
Bd2/Sh1	3.55	1.68
BH1	28.4	27.2
BH2	28.7	21.5
BH3	52.9	36.7
B/F	0.55	0.35
Br	33.2	23.8
Br/Ht	0.35	0.27
Cl1	51.5	37.4
Cl1/Bd1	0.39	0.15
Cl2	79.6	40.4
Cl2/Bd2	0.36	0.09
D	15.5	2.99
F	392.	297.
F/Cl1	7.75	3.91
GB	87.4	83.9
GB/B	0.42	0.18
GBW	43.8	38.6
GBW	43.8	38.6
GBW/GB	0.55	0.13
Ht	102.	26.0
Ht/D	6.83	2.08
Ln	450.	315.
Ln/Br	14.7	4.56
RB/B	0.60	0.17
RB	116.	52.0
RBW	175.	126.
RBW/SD	0.10	0.10
RBWH1	62.1	59.7
RBWH2	45.6	33.7
RBWH3	67.7	46.9
S/RB	72.7	22.1
SD/B	20.4	8.74
SD/BH1	29.8	14.8
SD/BH2	17.8	10.3
SD/BH3	13.5	7.31
SD/S	0.27	0.07
Sh1	71.1	37.4
Sh1/Bd1	0.61	0.15
Sh2	137.	93.3
SU/BH1	56.4	24.7
SU/BH2	52.6	20.6
SU/BH3	48.0	17.3

Notation as in List of Symbols

Table 4. Significant treatment effects upon cane components.

Source	Variable	Stratified Means			
Cane		C1	C2		
Thinning	*HT	108.	97.		
(C)	*Br/Ht	0.31	0.38		
	*Cl2	74.	85.		
	**Cl2/Bd2	0.35	0.38		
Top		T1	T2		
Thinning	*Br	37.	30.		
(T)	*Br/Ht	0.38	0.31		
	*Ln	498.	401.		
	*B/F	0.60	0.50		
	*S/B	76.	69.		
	*SUH1	60.	53.		
	**SDH3	15.	12.		
	**SUH3	51.	45.		
	*Cl2/Bd2	0.35	0.37		
C X T		C1,T1	C1,T2	C2,T1	C2,T2
	*SDH2	21.	16.	16.	18.
	*SDH3	16.	11.	14.	13.
	*SUH3	55.	43.	48.	47.
	**SD/S	0.29	0.26	0.25	0.28
	**SD/B	24.	19.	19.	20.
Daminozide		D1	D2	D3	
Deviations	*Ht	106.	97.	104.	
Deviations	*Ht/D	7.1	6.4	7.0	
Linear	*F	440.	399.	337.	
Deviations	*RB/B	0.56	0.56	0.62	
Deviations	*SDH2	18.	20.	16.	
Deviations	**SD/S	0.27	0.29	0.25	
Deviations	*SD/B	20.	22.	19.	
Linear	*RBW/Sd	0.09	0.08	0.12	
Deviations	*GB/B	0.42	0.45	0.38	
Deviations	*GBW/Ca	44.0	51.1	36.0	
Deviations	*GBW	44.4	50.9	36.1	
Linear	**Bd2/Sh1	3.2	3.5	4.0	
Linear	*Cl2	74.	78.	88.	
Linear	**Sh2	121.	139.	150.	

* $0.01 < P < 0.05$
** $P < 0.05$
C1 not cane thinned, C2 cane thinned, T1 not top thinned, T2 top thinned, D1 0 ppm daminozide, D2 5000 ppm daminozide, D3 10,000 ppm daminozide
Notation as in List of Symbols

therefore effective in reducing the total number of seeds set but not the number which finally developed. Numbers of both seed types were diminished in the third harvest by top thinning which indicates that this treatment limited development especially during the later part of the bearing period.

Significant interactions provide further evidence that top thinning limited development while cane thinning had positive effects. Top thinning applied without cane thinning reduced several seed numbers: SDH2, SDH3, SUH3, SD/S and SD/B (Table 4). With cane thinning the reduction was less or even reversed slightly. One explanation is that cane thinning removed weak canes which acted as sinks for growth substrates. Better light penetration might have increased photoynthesis in canes remaining after pruning thus reducing competition for photosynthate.

Daminozide treatments had many apparent effects. The number of buds per shoot in 1981 (Bd2/Sh1), and cluster and shoot numbers in 1982 (Cl2 and Sh2) increased with the concentration of daminozide applied (Table 4). These findings are similar to those of other workers (Hapitan et al., 1969; Gough et al., 1978a, 1978b). Significant deviations effects indicate quadratic or higher order responses to daminozide. These were found for cane height (Ht) and the ratio of cane height to diameter (Ht/D) even though these components were measured before daminozide was applied. The 5000 ppm treatment appears unaccountably to have been applied to bushes with a short mean cane height creating spurious significance for this treatment. Other components exhibited similar responses to daminozide (Table 4) but these might have been related to Ht or Ht/D and are considered unreliable.

4.2 Treatment effects upon bush components

Bush component means and standard deviations (Table 5) are provided for reference and to establish typical values encountered in this study. Cane thinning was effective in reducing the number of canes per crown area (Ca/Cr) and also reduced canopy area (Cp) (Table 6). New cane emergence (CaN) was enhanced in response to cane thinning. Top thinning reduced developed seed number per berry in the third harvest (SDH3/BH3). This is further evidence that top thinning limited development especially later in the bearing period (Table 6).

There was a significant interaction between the two pruning treatments as they affected canopy area (Cp). Top thinning reduced Cp in bushes which were not cane-thinned, while in cane-thinned bushes top thinning increased Cp. Combining both types of pruning promoted new shoot growth which extended further than the growth which was removed by top thinning.

Table 5. Means and standard deviations of bush components.

	Means	Standard Deviations
B	6038.	1903.
B1	864.7	277.6
B2	868.5	272.6
B3	1599.	403.3
Br	1015.	382.4
Br/Cp	.0385	.0159
Cl1	1577.	519.0
Ca	30.71	6.669
Ca/Cp	.0012	.0003
Ca/Cr	0.037	0.009
CaN	6.667	3.158
Cl2	2457.	767.0
Cp	27280	5823.
Cr	852.1	175.3
F	12048	4280.
GB	2706.	1156.
GBW	1353.	538.9
Ln	13559	3860.
RB	3332.	911.5
RBW	5308.	1570.
RBW1	1884.	634.4
RBW2	1385.	462.9
RBW3	2039.	562.4
Sh1	2195.	675.5
Sh2	4217.	1225.

Notation as in List of Symbols

Table 6. Significant treatment effects upon bush components

Source	Variable	Stratified Means			
Cane Thinning (C)		C1	C2		
	*Ca/Cr	0.041	0.033		
	**Cp	28680	25880		
	**CaN	5.2	8.1		
Top Thinning (T)		T1	T2		
	*SDH3/B	14.7	11.4		
C X T		C1,T1	C1,T2	C2,T1	C2,T2
	*Cp	30410	26950	25540	26230
Daminozide		D1	D2	D3	
Deviations	*CaN	7.	5.	8.	
Linear	*Cp	28910	27170	25760	

* 0.01 < P < 0.05
** P < 0.01
C1 not cane thinned, C2 cane thinned, T1 not top thinned, T2 top thinned, D1 0 ppm daminozide, D2 5000 ppm daminozide, D3 10,000 ppm daminozide
Notation as in List of Symbols

The reduction in canopy area (Cp) with increasing concentrations of daminozide (Table 6) might have resulted from a reduction in shoot elongation. This effect of daminozide has been found by other researchers (Hapitan et al., 1969; Gough et al., 1978a, 1978b) but was not tested in this study. There was a deviations effect of daminozide upon CaN but, as explained in section 4.1, the genuineness of this effect is doubtful.

4.3 Yield components of ripe berry weight per cane

Simple linear regressions of ripe berry weight per cane (RBW/Ca) upon fruit set (B/F), seeds per berry (S/RB) and berry enlargement per developed seed (RBW/SD) were almost perfect (Table 7). Regression coefficients were positive for B/F and S/RB, and negative for RBW/SD.

The R^2 for fruit set (B/F) was less in the forward SYCA (Table 8) than in the simple linear regression (Table 7). This indicates that earlier components affected yield through their influence upon B/F. When B/F was considered a yield variable, 16% of its variability could be attributed to earlier components. Branches per height (Br/Ht) accounted for half of this amount and 13% of the variability in ripe berry yield (RBW/Ca) appears to have resulted from Br/Ht affecting B/F. The remaining 84% of the variability in B/F was caused

Table 7. R^2's from simple linear regressions of yields per cane upon their components.

Yield Variables	Independent Variables											
	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Cl1/Bd1	F/Cl1	B/F	RB/B	S/RB	SD/S	RBW/SD
RBW	1	−1	12	−2	0	17	3	98	−5	99	−29	−99
	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Cl1/Bd1	F/Cl1	B/F	GB/B	GBW/GB		
GBW	0	0	10	−1	0	20	1	66	30	−21		
	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Sh1/Bd1	Bd2/Sh1	Cl2/Bd2				
Cl2	11	−3	8	1	−1	0	7	47				

R^2's $\geq$ 2% are significant P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

Table 8. Forward SYCA for ripe berry weight per cane.

	Total	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Cl1/Bd1	F/Cl1	B/F	RB/B	S/RB	SD/S	RBW/SD
						Independent	Variables						
Ht/D	29	-29	--	--	--	--	--	--	--	--	--	--	--
Br/Ht	22	12	-10	--	--	--	--	--	--	--	--	--	--
Ln/Br	9	-2	-0	-7	--	--	--	--	--	--	--	--	--
Bd1/Ln	49	-1	-2	-17	-29	--	--	--	--	--	--	--	--
Cl1/Bd1	26	-0	0	11	5	14	--	--	--	--	--	--	--
F/Cl1	10	1	3	0	1	5	-0	--	--	--	--	--	--
B/F	16	-1	-0	8	-1	-1	4	1	--	--	--	--	--
RB/B	9	-0	-0	-2	0	0	-3	0	-3	--	--	--	--
S/RB	100	0	-0	9	0	2	6	3	80	0	--	--	--
SD/S	42	0	1	1	0	0	0	-1	-32	-7	0	--	--
RBW/SD	100	1	-0	-9	-0	2	-6	2	-79	-0	-0	-0	--
RBW/Ca	100	1	0	13	0	4	6	3	74	0	0	0	0

R^2's $\geq$ 2% are significant P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

either by external uncontrolled factors which affected pollination such as bee visits or weather, or from nutritional, physiological or earlier component effects which were not considered in the model. After earlier components were considered, B/F accounted for all residual variation in RBW/Ca (Table 8). This implies that yield may be amenable to manipulation by controlling fruit set.

The number of seeds per berry (S/RB) was found to be positively related to fruit set (B/F) in the forward SYCA (Table 8). Nutrition or pollinator efficiency might have increased berries set and seeds per berry at the same time. The portion of seeds which developed (SD/S) and fruit weight per developed seed (RBW/SD) were negatively related to fruit set (B/F) (Table 8) and seeds per berry (S/RB) (Table 9). This indicates that fruit and seed development compensated for fruit and seed set.

Results of the backward SYCA (Table 9) provide a better picture of the relations between B/F, S/RB, SD/S and RBW/SD. Fruit weight per developed seed (RBW/SD) accounted for almost all of the yield variability when included first in the regression and the relation was negative. This occurred because compensations by fruit and seed development for fruit and possibly seed set were not strong enough to completely diminish the positive effects of fruit and seed set upon yield (Tables 8 and 9).

From these results and interpretations of SYCA it is

Table 9. Backward SYCA for ripe berry weight per cane.

	Total	Independent Variables D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Cl1/Bd1	F/Cl1	B/F	RB/B	S/RB	SD/S	RBW/SD
Ht/D	29	-29	--	--	--	--	--	--	--	--	--	--	--
Br/Ht	22	1	-21	--	--	--	--	--	--	--	--	--	--
Ln/Br	9	-1	-1	-7	--	--	--	--	--	--	--	--	--
Bd1/Ln	49	0	-1	-32	-16	--	--	--	--	--	--	--	--
Cl1/Bd1	26	0	4	18	-1	3	--	--	--	--	--	--	--
F/Cl1	10	1	3	0	4	2	0	--	--	--	--	--	--
B/F	16	0	0	2	-3	0	10	1	--	--	--	--	--
RB/B	9	0	0	0	0	1	-2	0	-6	--	--	--	--
S/RB	100	0	0	0	0	0	1	0	93	-6	--	--	--
SD/S	42	1	0	0	1	0	1	0	-2	-7	-30	--	--
RBW/SD	100	0	0	0	0	0	0	0	0	0	-72	27	--
RBW/Ca	100	0	0	1	0	0	0	0	0	0	0	0	-99

R^2's $\geq$ 2% are significant P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

impossible to distinguish whether yield was determined by fruit set (B/F) or seeds per berry (S/RB). Results of the simple linear regressions (Table 7) show that both B/F and S/RB were almost perfect predictors of yield. These two components were positively related probably because another factor affected them both similarly. This presents a problem in interpretating the SYCA results since the assumption that component collinearity is due to sequential development was possibly not the case. Although B/F was indicated as the yield-determining component in the forward SYCA, it is possible that S/RB was actually more important in determining yield and its effect was attributed to B/F because of their collinearity. It is understandable that fruit set might have determined yield by increasing berry number without total compensatory loss through reduction in berry size. But it is also possible that set seeds stimulated berry enlargement which in turn determined yield. This theory would have been tested if effects of seeds per berry upon fruit size, and fruit size upon final yield could be determined from the analysis. But the nature of the component ratios constructed for the model prevented the necessary regressions from being performed.

4.4 Yield components of green berry weight per cane

Simple linear regressions (Table 7) found that green berry yield (GBW/Ca) was inversely related to green berry size (GBW/GB), and was directly related to earlier components: branches per height (Br/Ht), the portion of buds which developed into clusters (Cl1/Bd1), fruit set (B/F) and the portion of berries which did not ripen (GB/B). Fruit set (B/F) had the greatest R^2 and was also the most important yield component in the forward analysis (Table 10). Other components, branches per cane height (Br/Ht), the portion of buds which became clusters (Cl1/Bd1), the portion of berries which remained green (GB/B) and green berry size (GBW/GB), also contributed substantially to yield in the forward analysis and had positive regression coefficients.

In the backward analysis (Table 11), all variability in green berry yield (GBW/Ca) was accounted for by the last three components: B/F, GB/B and GBW/GB. Br/Ht and Cl1/Bd1 therefore affected yield by contributing to these three. There are several possible ways in which this occured. Fruit set (B/F) was promoted by branches per height (Br/Ht) while green berry size (GBW/GB) compensated for both Br/Ht and the portion of buds which became clusters (Cl1/Bd1) (Tables 8 and 10). Cl1/Bd1 also contributed a small amount to the portion of berries which remained green (GB/B). It is impossible to distinguish the importance of each of these effects upon yield from SYCA results.

The portion of berries which did not ripen (GB/B) was an important component of green berry yield and little of

Table 10. Forward SYCA for green berry weight per cane.

	Total	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Cl1/Bd1	F/Cl1	B/F	GB/B	GBW/GB
					Independent Variables						
GB/B	6	0	0	-0	1	-0	4	-0	-1	--	--
GBW/GB	36	-0	-0	-8	0	4	-21	-0	-3	-2	--
GBW/Ca	100	1	0	11	0	3	10	1	46	10	20

R^2's $\geq$ 2% - significant at P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

Table 11. Backward SYCA for green berry weight per cane.

	Total	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Cl1/Bd1	F/Cl1	B/F	GB/B	GBW/GB
					Independent Variables						
GB/B	6	0	0	0	1	0	5	0	0	--	--
GBW/GB	39	1	0	0	0	0	-19	0	-13	-6	--
GBW/Ca	100	0	0	0	0	0	1	0	58	20	-21

R^2's $\geq$ 2% - significant at P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

its variability could be attributed to earlier cane components (Tables 10 and 11). Possible sources of the variability in berry ripening were nutrition, fruit positioning on canes, cane leaf area, light exposure to leaves or fruit, or other morphological properties which were not included in the model.

Yield (GBW/Ca) was directly related to green berry size (GBW/GB) in the forward analysis (Table 10) and inversely related but in the backward analysis (Table 11). This was the result of green berry size (GBW/GB) partially compensating for some earlier components which promoted green fruit yield: the portion of buds which became clusters (Cl1/Bd1), fruit set (B/F) and the portion of berries which did not ripen (GB/B). In the forward SYCA (Table 10) the total effects of these earlier components, including compensation by GBW/GB, were considered before GBW/GB was fitted. Residual variability in yield was then found to be positively related to GBW/GB. Green berry enlargment therefore had potential to contribute to yield of green berries.

Fruit set (B/F) had little effect upon the portion of berries which did not ripen (GB/B) but did contribute highly to green berry yield (GBW/GB) (Tables 10 and 11). It is therefore reasonable to believe that fruit set was positively related to green berry number. Large R^2 values for B/F indicate that it was the most important component of green fruit yield. But since B/F was also strongly related to ripe fruit yield, high yields of both ripe and green fruit were produced when fruit set was high. This suggests that ripening was important although the portion of berries which ripened (RB/B) hardly contributed to ripe fruit yield variability.

4.5 Yield components of the number of clusters per cane in 1982

Cluster yield in 1982 (Cl2/Ca) was most strongly related to the portion of buds which differentiated into clusters in 1981 (Cl2/Bd2) (Table 7). Cluster yield was also positively related to the number of buds per shoot (Bd2/Sh1) (Table 7).

The portion of buds which differentiated into clusters (Cl2/Bd2) contributed less to cluster yield in the forward SYCA than in the backward or simple regression analyses (Tables 7, 12 and 13). It can be inferred that an earlier component, the number of buds per shoot (Bd2/Sh1), contributed to cluster yield through Cl2/Bd2.

In the backward SYCA, cane diameter (D/Ca) contributed 8% of the cluster yield variability which was direct and independent of later components (Table 13). Cane diameter did not contribute to the portion of buds which became clusters (Cl2/Bd2). Therefore the effect of cane diameter

Table 12. Forward SYCA for the number of clusters per cane in 1982.

	Total	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Sh1/Bd1	Bd2/Sh1	Cl2/Bd2
					Independent Variables				
Sh1/Bd1	21	0	-0	-10	-0	-11	--	--	--
Bd2/Sh1	48	- 1	-0	-28	-0	-6	-13	--	--
Cl2/Bd2	13	1	1	2	1	0	2	8	--
Cl2/Ca	100	11	0	4	4	3	4	51	23

R^2's ≥ 2% - significant at P=0.05
Signs are those of regressions and not of associated R^2
Notation as in List of Symbols

Table 13. Backward SYCA for the number of clusters per cane in 1982.

	Total	D	Ht/D	Br/Ht	Ln/Br	Bd1/Ln	Sh1/Bd1	Bd2/Sh1	Cl2/Bd2
					Independent Variables				
Sh1/Bd1	21	0	-3	-16	0	-2	--	--	--
Bd2/Sh1	48	0	-11	-33	3	1	0	--	--
Cl2/Bd2	13	0	0	5	1	0	3	4	--
Cl2/Ca	100	8	9	32	-1	-1	0	2	47

R^2's ≥ 2% - significant at P=0.05
Signs are those of regressions and not of associated R^2
Notation as in List of Symbols

probably had little to do with water or nutrient conduction. It is likely that cane diameter was proportional to cane age and size. This could affect the yield of clusters without necessarily affecting component ratios.

The number of buds per shoot (Bd2/Sh1) compensated directly for cane height per unit of diameter (Ht/D) and the number of branches per height of cane (Br/Ht) (Table 13). This implies that tall slim canes with extensive branching had shoots with fewer leaves and therefore fewer buds in 1981. These compensations were taken into account when the bud number per shoot (Bd2/Sh1) was included in the backward SYCA for cluster yield (Cl2/Ca) (Table 13). Ht/D and Br/Ht were then shown to have potential to affect cluster yield in the absence of compensation by Bd2/Sh1.

4.6 Yield components of ripe berry weight, green berry weight and the numbers of clusters per bush

Results of simple linear regressions and backward and forward analyses for bush yields of ripe berries (RBW/Bu), green berries (GBW/Bu) and clusters (Cl2/Bu) were very similar (Tables 14-17). Individual cane yields of ripe berries (RBW/Ca) green berries (GBW/Ca) and clusters (Cl2/Ca) had the greatest influence upon bush yields. Crown area (Cr) was positively related to yield in the backward analyses (Tables 15-17) but was insignificant in

Table 14. R^2's from simple linear regressions of yield per bush upon its components.

Yield Variables	Independent Variables		
	Cr	Ca/Cr	RBW/Ca
RBW	3	12	42
	Cr	Ca/Cr	GBW/Ca
GBW	8	9	23
	Cr	Ca/Cr	C12/Ca
C12	3	21	52

R^2's $\geq$ 16% are significant at P=0.05
Notation as in List of Symbols

Table 15. Forward and backward SYCA for ripe berry weight per bush.

		Total	Cr	Independent Variables Ca/Cr	RBW/Ca
Ca/Cr	Forward	33	-33	--	--
	Backward	33	-33	--	--
RBW/Ca	Forward	6	-3	-3	--
	Backward	6	-6	0	--
RBW/Bu	Forward	100	3	30	67
	Backward	100	42	14	44
Minimum R^2			16	17	18

Minimum R^2 - minimum R^2 for significance at P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

Table 16. Forward and backward SYCA for green berry weight per bush.

		Total	Independent Variables Cr	Ca/Cr	GBW/Ca
GBW/Ca	Forward	1	0	1	--
	Backward	1	1	0	--
GBW/Bu	Forward	100	8	32	61
	Backward	100	23	7	70
Minimum R^2			16	17	18

Minimum R^2 - mininum R^2 for siginificance at P=0.05
Notation as in List of Symbols

Table 17. Forward and backward SYCA for the number of clusters per bush in 1982.

		Total	Independent Variables Cr	Ca/Cr	C12/Ca
C12/Ca	Forward	4	-3	1	--
	Backward	4	-1	3	--
C12/Bu	Forward	100	3	47	50
	Backward	100	36	12	52
Minimum R^2			16	17	18

Minimum R^2 - minimum R^2 for significance at P=0.05
Signs are those of regressions and not of associated R^2
Notation as in List of Symbols

the forward analyses because the number of canes per crown area (Ca/Cr) compensated and diminished the net effect of crown area upon yield. The number of canes per crown area contributed more to yield in the forward analyses which measured its effect independent of crown area.

4.7 Effects of pruning treatments upon component contributions to yield and later components

Results of SYCA were similar when it was applied to bushes and canes which received different treatments. R^2's for bush yield components were not significantly different among treatment factor levels but there were only 12 replicates per factor level. Replication was ten times greater for each cane SYCA and so detection of R^2 differences was more powerful. Significant differences were found (Tables 18 and 19) but no consistant pattern was noticable. Treatment mode of action could not be determined by comparing individual R^2's. Even though significant differences were found, the results as a whole were difficult to intepret.

4.8 Changes in fruit properties with harvest

Fruit properties were affected by harvest and treatment interactions with harvest (Table 20). Berries

Table 18. R^2 contributions to yield and yield components which are significantly different due to cane thinning.

Dependent Variable	Independent Variable	Thinned	Not thinned
FORWARD SYCA			
Ln/Br	Br/Ht	-19	0
S/RB	B/F	88	68
RBW/SD	B/F	-88	-67
GB/B	Cl1/Bd1	-8	0
GB/B	B/F	0	-9
GBW/Ca	B/F	39	61
GBW/Ca	GB/B	42	1
Cl2/Ca	D/Ca	29	1
Cl2/Ca	Ln/Br	1	14
BACKWARD SYCA			
Br/Ht	Ht/D	-31	-10
Ln/Br	Br/Ht	-21	0
Bd1/Ln	Ln/Br	-7	-26
Cl1/Bd1	Ln/Br	-7	0
F/Cl1	Ht/D	0	7
B/F	Cl1/Bd1	4	19
Gb/B	B/F	0	-7
GBW/Ca	B/F	43	84
GBW/Ca	GB/B	28	-1
Bd2/Sh1	Ht/D	-19	-3
Bd2/Sh1	Br/Ht	-26	-46

R^2's $\geq$ 2% are significant at P=0.05
R^2's listed for each treatment are different according to a Z-test at P=0.05
Notation as in List of Symbols

Table 19. R^2 contributions to yield and yield components which are significantly different due to top thinning.

Dependent Variable	Independent Variable	Thinned	Not thinned
FORWARD SYCA			
Ht/D	D/Ca	38	20
SD/S	B/F	39	17
GBW/Ca	B/F	54	30
Bd2/Sh1	Br/Ht	16	39
BACKWARD SYCA			
RB/B	Cl1/Bd1	0	-11
SD/S	S/RB	-39	-18
RBW/SD	S/RB	-63	-86
RBW/SD	SD/S	36	14
GB/B	Cl1/Bd1	0	18
GBW/Ca	B/F	63	44
GBW/Ca	GB/B	14	35

R^2's $\geq$ 2% are significant at P=0.05
R^2's listed for each treatment are different according to a Z-test at P=0.05
Notation as in List of Symbols

Table 20. Significant changes in fruit properties with harvest.

Variable	Source	Stratified Means					
		H1	H2	H3			
RBW	HD	62.1	45.6	67.2			
		H1	H2	H3			
RB	HL	28.4	28.7	52.9			
	HD	"	"	"			
		H1	H2	H3			
S	HD	2824	2217	2750			
		H1	H2	H3			
SD	HL	1003	581	764			
	HD	"	"	"			
		T1,H1	T1,H2	T1,H3	T2,H1	T2,H2	T2,H3
	T X HL	962	639	881	1043	524	648
		H1	H2	H3			
SU	HL	1821	1635	3514			
	HD	"	"	"			
		T1,H1	T1,H2	T1,H3	T2,H1	T2,H2	T2,H3
	T X HL	1760	1721	3929	1883	1550	3100
		H1	H2	H3			
RBW/B	HL	1.95	1.53	1.27			
	HD	"	"	"			
		H1	H2	H3			
S/B	HL	86.2	70.4	61.5			
		H1	H2	H3			
SD/B	HL	29.8	17.8	13.5			
	HD	"	"	"			
		H1	H2	H3			
SU/B	HL	56.4	52.6	48.0			

HL harvest linear, HD harvest deviations, H1 first harvest,
H2 second harvest, H3 third harvest, T top thinning,
T1 not top thinned, T2 top thinned
Notation as is List of Symbols

from the first harvest were large, few and contained many seeds of both sizes. Berries from the second harvest were small, few and contained fewer developed seeds than those from the first harvest. The last harvest contained the most berries but they were small with few developed, undeveloped and total seeds. The high yield in the first harvest resulted from few but large berries while the high yield in the last harvest resulted from many small berries.

Changes in the portion of seeds which developed (SD/S) and berry size (RBW/B) with harvest were similar. This might indicate that developing seeds stimulated fruit enlargement as suggested in a report from an early study (Meader and Darrow, 1944). It is also possible that climate, nutrition or morphological components such as fruit set or leaf area affected berry enlargement and seed development similarly. After the first harvest the weather became hotter and dryer and this continued through the third harvest. Limited water availability could explain the smaller berry size and perhaps the lesser number of developed seeds. But since both developed and undeveloped seeds decreased with harvest the decline was probably controlled by a factor which operated during pollination. One possibility is that the availability of substrates needed for seed set and fruit development were diminished by the fruits and seeds which developed first.

Interactions between top thinning and harvest (Table 20) show that the decline in developed seed number (SD) with harvest was more pronounced in top-thinned bushes than in those not thinned. This is further evidence that top thinning limited development.

4.9 Biennial bearing tendencies

When SYCA was used to detect stages of fruiting which affected bud differentiation and cluster yield in the following year, significant regressions were mostly positive (Table 21). For example, the portion of berries which ripened (RB/B) had the greatest R^2 and a positive regression coefficient and so conditions which favored ripening also favored reproductive bud differentiation. One explanation is that the availability of nutrients or other substrates affected both components similarly. The greater R^2 for canes from bushes which were not cane-thinned might have resulted from limited photosynthesis due to shading in unthinned bushes. In this case ripening and bud differentiation would be controlled by sugar availability to a greater degree than in thinned bushes where other factors might be more limiting.

4.10 Relations between canopy area and bush components

Effects of canopy area were difficult to detect on the

Table 21. Results of forward and backward SYCA for effects of fruiting in 1981 upon cluster yield in 1982.

		Independent Variables							
		Cl1/Bd1	F/Cl1	B/F	RB/B	S/RB	SD/S	RBW/SD	RBW/Ca
ALL COMBINED	Forward	-1	1	1	9	-1	0	2	-1
	Backward	0	1	1	9	1	-1	1	1
CANE THINNED	Forward	1	5	1	2	3	0	1	1
	Backward	0	5	2	3	0	0	4	0
NOT CANE THINNED	Forward	0	1	3	16	0	0	1	-1
	Backward	0	0	1	15	2	-2	0	2
TOP THINNED	Forward	0	1	5	10	-1	0	6	0
	Backward	0	0	2	9	3	-1	2	5
NOT TOP THINNED	Forward	-3	1	0	8	-1	0	0	0
	Backward	3	3	0	9	0	0	1	0

R^2's $\geq$ 2% are significant P=0.05
Signs are those of regressions and not the associated R^2
Notation as in List of Symbols

basis of only 24 bushes, nevertheless some components were affected significantly (Table 22). Flower number (F), berry number (B) and green berry yield (GBW) were positively related to canopy area for certain treatments. These relations may reflect bush size rather than effects of light exposure. However, the portion of berries which ripened (RB/B) was positively related to canopy area in bushes which were not top-thinned. This probably resulted from effects of light exposure to leaves and berries since thinned bushes would not be expected to benefit from a more extensive habit if remaining shoots were adequately exposed to light. As top thinning did not affect the mean for RB/B, ripening was generally best in extensive bushes which were not top-thinned and worst in narrow bushes which were not top-thinned.

Crown area and canopy area were positively correlated (not tabulated). It is therefore possible that regressions of components upon canopy area resulted partially from effects of crown area.

4.11 Effects of bush components upon the formation of new canes

Several regressions of new cane number (CaN) upon bush components were significant (Table 23). CaN was positively related to four components: the diameter of existing canes

Table 22. Significant regressions of components upon canopy area.

Dependent Variable	Treatment	R^2	Regression Coefficient	Intercept
F	not top thinned	35*	37.0	1540
	0 ppm daminozide	53*	79.0	-9635
B	all combined	21*	14.9	1975
	not cane thinned	32*	14.3	2245
	0 ppm daminozide	71**	33.4	-3525
RB/B	not top thinned	46*	57×10^{-5}	0.700**
GBW	all combined	57*	-68×10^{-7}	0.577
	not cane thinned	34*	5.0	-0.250
	not top thinned	44*	5.6	-66.20
	0 ppm daminozide	72**	10.6	-581.9

* $0.01 < P < 0.05$
** $P < 0.05$
Notation as in List of Symbols

(D/Ca), shoot numbers in 1981 (Sh1) and 1982 (Sh2) and cluster number in 1982 (Cl2). One explanation of these results is that vigorous or well established bushes produced more new growth of all types.

It was more difficult to detect significant regressions within individual pruning treatment factor levels with only twelve bushes per level. The relation between CaN and the number of shoots in 1981 (Sh1) was highly significant in cane-thinned bushes but not in controls (Table 23). Cane thinning therefore promoted the production of new canes (Table 7) and the number which emerged was proportional to the number of vegetative shoots on remaining canes (Table 23). Top thinning had the opposite effect. There was a significant relation between new cane number (CaN) and shoot number (Sh1) in bushes which were not top-thinned but not in thinned bushes. The vegetative buds removed in top thinning did not result in a significant reduction of their numbers (P=0.15) but removal of a few potential shoots might have been enough to affect new cane emergence. A similar situation was found when CaN was regressed with the number of clusters produced in 1982 (Cl2) (Table 23). CaN was significanty related to Cl2 in cane-thinned bushes but not in controls. Cane thinning seems to have induced vigor and promoted CaN and Cl2 at the same time. This same relation between CaN and Cl2 was found in bushes which were not top-thinned but not

Table 23. Significant regressions of new cane number upon bush components.

Independent Variable	Treatment	R^2	Regression Coefficient	Intercept
Ca	cane thinned	40*	0.296	-1.11
D/Ca	all combined	22*	0.014	0.116
Sh1	all combined	26**	0.002	1.39
	cane thinned	47**	0.003	1.00
	not top thinned	38*	0.003	-0.622
SD1	all combined	17*	-0.327	15.4**
	0 ppm daminozide	53*	-0.405	18.4**
SU2/RB3	not cane thinned	36*	-0.210	15.5**
	0 ppm daminozide	79**	-0.402	26.6**
SD2/RB3	0 ppm daminozide	56*	-0.456	14.5**
SU3/RB3	0 ppm daminozide	58*	-0.199	16.1**
SD3/RB3	not top thinned	37*	-0.757	17.1**
	0 ppm daminozide	71**	-0.631	15.1**
C12	all combined	34**	0.002	0.760
	cane thinned	40*	0.002	2.19
	not top thinned	56**	0.003	-2.56
	0 ppm daminozide	54*	0.003	-0.0103
Sh2	all combined	17*	0.001	2.18
Cr	cane thinned	35*	0.012	-1.03

* $0.01 < P < 0.05$
** $P < 0.01$
Notation as in List of Symbols

in thinned bushes. Again top thinning appears to have reduced vigor.

Regressions of CaN upon existing cane number (Ca), canopy area (Cp) and crown area (Cr) were positive in cane-thinned bushes. More new canes were produced by bushes with extensive crown and canopy areas for light penetration and many canes selectively left for photosynthesis.

The negative relation between CaN and the number of undeveloped seeds per berry in the second harvest (SUH2/BH2) (Table 23) may indicate that nutrients or other growth substrates were limiting seed development and emergence of new canes at the same time. For example, bushes of poor vigor would have many seeds remaining undeveloped and few new canes. There was a negative relation between CaN and the number of developed seeds per berry in the third harvest (SDH3/BH3). Since new canes emerged before the third harvest it is possible that new cane development competed with development of seeds.

New cane emergence in daminozide treated bushes was unrelated to bush components while emergence in control bushes was significantly related to some components (Table 23). It is possible that daminozide affected newly emerging canes since it was applied at the time of emergence. Further discussion of this possible effect is not warranted since there was an unreliable deviations effect of daminozide upon CaN (Table 7).

5. SUMMARY OF GROWTH AND YIELD RELATIONS

Ripe berry yield was determined either by fruit set or the number of seeds per berry. These two components were positively related indicating that both were affected similarly by another factor such as pollination, nutrition or a component such as leaf area which was not included in the model.

Both ripe and green berry yields were related to fruit set. Since green berry yield was inversely related to green berry size, high yields of green fruit occurred when berries did not enlarge and ripen. Although ripening was unaffected by earlier cane components, canopy area was related to ripening in bushes which were not top-thinned.

Berry size and numbers of both developed and undeveloped seeds decreased at later harvests. These harvest trends, which are similar to those found by other workers (Darrow, 1958; Moore et al., 1972), might have resulted from effects of climate, hormonal control or availability of nutrients or sugars. Further experiments are needed to determine if seeds influence berry enlargment.

Cluster yield was determined by the number of buds initiated and the portion which differentiated into reproductive buds. Biennial bearing tendencies could not be detected and it is reasonable to believe that flowering and fruiting did not influence reproductive bud differentiation.

Effects of cane thinning were beneficial while top thinning seemed to limit growth. Cane thinning enhanced new cane emergence, reproductive bud differentiation in 1981 and cluster yield in 1982 but yield of ripe berries in 1981 remained unaffected. Top thinning enhanced reproductive bud differentiation in 1981 but cluster yield was unaffected in 1982. Components diminished by top thinning included fruit set and several seed counts. Canopy area enhanced ripening only in bushes which were not top thinned and the decline in some seed counts with harvest was more pronounced in top-thinned bushes. It would be interesting to investigate the long term effects of cane thinning without top thinning.

Results of this study suggest that enhancement of yield in a given year would be most easily attained by increasing fruit or seed set. Cultural practices such as supplying bees or applying sufficient fertilizers may be effective in manipulating these yield components. Cane thinning appears to have potential to increase yield in years later than the year it is applied.

Previous studies which related blueberry growth and yield considered the thickness and length of the bearing laterals. These affected reproductive bud development (Shutak et al., 1957), cluster and shoot numbers (Bowen and

Eaton, 1983; Filmer and Marucci, 1963; Gough et al., 1976), time of blossoming and berry size (Hindle et al., 1957a; Shutak et al., 1957). Yield components studied in this thesis did not include properties of the bearing laterals. These properties may have contributed to yield component variability which was not attributed to earlier components during regressions in which yield components were considered yield variables (Tables 8-13).

6. DISCUSSION OF SYCA

SYCA contributed much to the description of blueberry growth and yield relations in this thesis. However, clear interpretation of SYCA results was not permitted when the assumptions concerning collinearity were not met. In some cases it was more logical to assume that collinearity resulted from an external factor affecting components similarly rather than components affecting each other. If, for example, there were three such collinear components and only the second of these in the developmental series was important in determining yield, the first component would be indicated in the forward analysis and the third in the backward analysis. The second component might appear to have little or no effect upon yield. Regressions in which components were considered yield variables indicated which components were collinear. Simple linear regressions of yield upon each yield component indicated which components were related to yield, but important yield determining components could not be distinguished from possibly unimportant collinear ones.

During the writing of this thesis new ideas for using SYCA were brought forward. Listed below are those which either resulted from the interpretation of this work or resulted from other studies but would have provided better analysis techniques for this study.

1. Simple linear regressions of yield upon each

component may be useful in determining component mode of action upon yield. For example, an early component might affect yield by influencing a chain of later components. The forward analysis would indicate this early component as important and the backward analysis might indicate only the last of the affected components. Regressions of the later components upon earlier ones would reveal which components were affected by the important early component. Simple linear regressions of yield upon each component would indicate whether these effects possibly influenced yield.

2. Since yield variability is totally accounted for by variation in its components, treatments must affect yield by affecting yield components. This approach to determining treatment mode of action was taken recently by Eaton, Bowen and Jolliffe (1983) and provided the basis for a further analysis in which treatments and yield components are considered together. The analysis includes SYCA and ordinary analysis of variance procedures and was named two dimensional partioning (TDP).

3. External factors, such as climate or treatments, produce variation in yield components

which cannot be attributed to earlier components. This unexplained variation could be attributed to the appropriate factors by including the corresponding residual variables in TDP. These residual variables are simply the orthogonal variates obtained from multiple regressions of components upon developmentaly earlier ones.

4. It is possible to determine the amount of replication required to designate an R^2 of a particular size as significant. But when yield component models contain many components, R^2's tend to be small and it is possible to obtain R^2's which add to 100% but are all insignificant. In this thesis many components were handled by designating a yield component or independent variable of one model as the yield or dependent variable of another. This method of modelling in tiers seems to be a convenient way of dealing with many potential yield components.

5. So far, only the signs of regression coefficients produced in SYCA have been interpreted. However, the values of these coefficients correspond to exponents of the original untransformed component variables. These coefficients, known as allometric exponents

in allometry, may indicate curvilinear responses of yield to yield components.

Although SYCA did not provide a total picture of growth and yield relations in highbush blueberry, many relations were detected which had not yet been reported. This relatively new technique continues to be refined and expanded as further questions are asked about the origins of crop yield.

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