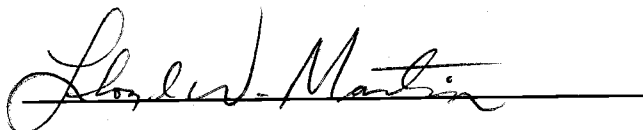AN ABSTRACT OF THE THESIS OF

Jeffery L. Olsen for the degree of Master of Science

in Horticulture presented on October 12, 1983.

Title: Yield Component and Growth Analyses of

Strawberries.

Abstract approved: _____

        Two studies were initiated in June of 1981

in order to gain greater understanding of the growth

and fruiting habits of field grown strawberries in

Oregon's Willamette Valley.

        Yield component analysis of 'Benton', Oregon's

leading cultivar and an advanced breeding selection,

'OR-US 4356' was conducted during the first (1981)

and second (1982) fruiting years. In each season,

the two genotypes produced essentially the same

yields/plant, averaging 0.82 kg in 1981 and 0.94 kg

in 1982. 'Benton' produced 25-30% more crowns/plant

than 'OR-US 4356'. 'Benton' had fewed trusses/

crown in 1981 (0.93 vs. 1.47) but in 1982 their

numbers were the same (1.5). 'OR-US 4356' had about

60% higher numbers of fruit/truss in each season. However, 'Benton' averaged 75% greater mean berry weight than 'OR-US 4356'. There was no significant difference in total achenes/berry between genotypes (202 in 1981 and 239 in 1982). Larger fruit had a greater number of achenes and linear regressions of berry weight versus achenes/berry were significantly different between genotypes in each season. 'Benton' had less achenes/gram fresh weight of berry (24 vs. 34) and achenes/cm^2 (10.6 vs. 14.0) than 'OR-US 4356'. This indicates that 'OR-US 4356' fell short of its yield potential due to its inability to reach maximum berry expansion.

Frequent sampling and functional growth analysis were used to quantify growth of field grown straw-berry plants ('OR-US 4681') during the summer of establishment and through flowering and fruiting the next spring. Plant dry weight and leaf area increased rapidly during mid-summer, but thereafter gains slowed and finally ceased in October. This was reflected in the absolute growth rate (AGR) which peaked at 1 g dry matter/day near September 1, then fell to zero by early October. Over this period, weekly mean temperature, solar radiation, and day-length decreased by 37%, 47% and 35% respectively. Relative growth rate (RGR) declined steadily from a

high of 44 mg/g/day at the end of June. Unit leaf

rate (ULR) showed a similar pattern, starting at

9 g/m^2/day. During the following April through

June, both plant dry weight and leaf area increased

at exponential rates. The growth environment

improved during this period and the AGR increased

continuously but RGR remained constant at 19 mg/g/day.

The rate of dry matter accumulation in fruit was

exponential, whereas that in leaf lamina and stems

(crowns plus petioles) showed linear increases.

Because of fruiting, a much smaller proportion of

dry matter was partitioned to leaves than during

plant establishment. However, ULR rose from 5.5

to 6.5 g/m^2/day, indicating that dry matter production

was relatively constant during flower and fruit

production.

YIELD COMPONENT AND GROWTH ANALYSIS

OF STRAWBERRIES

by

Jeffery L. Olsen

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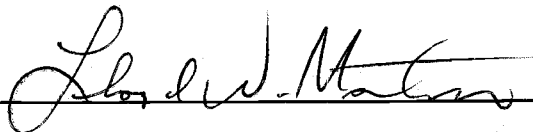
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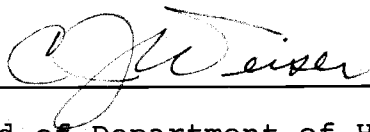the requirements for the
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Master of Science

Completed October 12, 1983

Commencement June 1984
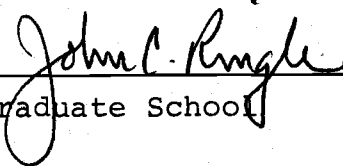
APPROVED:

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Professor of Horticulture in charge of major

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Head of Department of Horticulture

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Dean of Graduate School

Date Thesis is presented _____ October 12, 1983 _____

Typed by Margaret E. Considine for Jeffery L. Olsen

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

YIELD COMPONENT AND GROWTH ANALYSES

OF STRAWBERRIES

INTRODUCTION

Until very recently, quantitative investigations have only played a minor role in biology in comparison with the other sciences (Causton and Venus, 1981). In the last decade alone, Biological Abstracts list over 60,000 separate publications which specifically involve some aspect of 'plant growth' (Hunt 1982). A working definition of plant growth is provided by Hunt (1978) as "irreversible changes with time, mainly in size (however measured), often in form and occasionally in number". Plant growth is an intricate process involving multiple levels of organization, each affecting the other. Plant organization can be divided into seven levels: molecules, organelles, cells, tissue, component organs (individual leaves, etc.), main organ systems (root, stem, foliage, inflorescence), and the whole plant. Whole plant communities provide another level of research for plant biologists. The studies

contained herein focus on the main organ systems
and whole plant levels of the strawberry
(Fragaria X ananassa Duch.).

Two studies were initiated in June 1981 in
order to gain greater understanding of the growth
and fruiting habits of field grown strawberries
in Oregon. The amount of fruit produced by a
strawberry plant is determined by the multiplicative
effects of four yield components: the number of
crowns/plant, the number of trusses (inflorescences)/
crown, the number of berries/truss and the mean
berry weight. Dividing yield into component
parts may help in identifying factors which increase
or limit yields. In the first study, Oregon's
leading strawberry cultivar, 'Benton' and an
advanced selection from the breeding program,
'OR-US 4356', were chosen for a yield component
analysis because of their apparent contrast in
growth and fruiting habits.

A second study sought to quantify the plant
dry matter production and partitioning of another
advanced selection from the breeding program,
'OR-US 4681', during its establishment season and
initial fruiting year. The growth analysis involved
the destructive harvest of whole plants at 3-4 day

intervals over the course of the growing season.
Plant dry weights were recorded from these samples
and used to derive growth curves that model the
change in plant growth characteristics.

The plant analyst can employ various growth
analysis formulas to estimate the plant's biologi-
cal productivity and photosynthetic efficiency over
time. The applications of plant growth models
will likely increase as proliferation of computer
technology accelerates. Plant growth quantification
is vital to crop ecosystem modeling and pest
management planning. Quantification of strawberry
plant growth will also provide further insight into
the growth and yield of strawberries and may aid
plant breeders in developing improved cultivars.

LITERATURE REVIEW

Strawberry Yield Components

The strawberry of commerce, _Fragaria_ X _ananassa_
Duch., is an herbaceous perennial that produces
trifoliate, serrate leaves at close intervals on a
very shortened stem called a crown. Roots emerge
from the base of the crown while flowers are produced
at the terminal position on leaf axes.

The fruit yield of a strawberry plant
is determined by the multiplicative effects of four
components: the number of crowns/plant, the number of
trusses (inflorescences)/crown, the number of berries/
truss, and the mean berry weight (Hondelmann, 1965;
Webb, Purves, White, and Ellis, 1974). These morpho-
logical components of strawberry yield will be dis-
cussed individually herein.

The strawberry crown's vascular cylinder is
composed of a network of short anastomosing bundles
with leaf trace connections to the vascular cylinder
(Darrow, 1966). Thus, if one portion of the plant's
root system becomes injured or dies, the entire plant
will be affected, not just the part immediately ad-
jacent to the injury. Water and nutrients cross
freely through the vascular cylinder from any point

through the circumference of the crown. Shortened
photoperiods stimulate some axillary buds on the mother
crown to produce branch crowns which are morphologi-
cally identical to the main crown axis (Dana, 1981).
Guttridge (1955) suggests that branch crown buds
may grow into branch crowns any time of year
depending on general plant vigor. Branch crown buds
are formed after stolon (runner) differentiation (or
when stolon formation fails) and before the onset of
dormancy. When a branch crown is fully developed,
it produces leaves in the same progression as the
main crown from which it is functionally independent
(Jahn and Dana, 1970a). Branch crown formation is in-
hibited by suboptimal levels of nitrogen and phosphor-
ous (Abbott, 1968).

Mason and Rath (1980) found that in commercial
plantings of the cultivar 'Cambridge Favourite', crown
numbers accounted for more than 50% of the yield vari-
ance. Several studies document increased yields with an
increasing number of crowns per hectare (Rogers and
Mobilbowska, 1951; Anderson and Guttridge, 1976;
Waister, 1972; Harding, 1968; Williams, 1975;
Christopher and Shutak, 1938; Craig and Aalders, 1966;
Craig, Aalders and Leefe, 1973; Hondelmann, 1965).
However, inter-crown competition can lead to depressed
yields (Anderson and Guttridge, 1976; Christopher, 1941;

Christopher and Shutak, 1938; Crane and Haut, 1941;
Lorce, 1941; Childs, 1942; Ricketson, 1970; Albregts,
Howard and Poe, 1974). Anderson and Guttridge (1976)
found that parent plants without runners produced more
crowns/plant and trusses/plant than did plants with
runners in matted or spaced beds, presumably due to
reduced inter-crown competition.

Guttridge and Anderson (1981) further conclude
that crown number was not the most reliable guide for
assessing fruiting characteristics of a strawberry
clone. Rather, individual plant records of trusses/
crown or per plant, fruit/truss, and mean berry weight
were sufficient for analysis of fruit yields. But,
they caution that some direct measure of plant size
(not crown numbers) is essential to accurately assess
the yield characteristics and potential of a cultivar.
Research on runner removal, earlier time of rooting,
and nitrogen fertilization showed that the number of
trusses per plant was the most important determinant
of yield (Anderson and Guttridge, 1976; Breen and
Martin, 1981; Guttridge and Anderson, 1973; Webb and
White, 1971; Webb, White, and Ellis, 1973; Webb, Purves,
White, and Ellis, 1973). Exceptions to this occur
with some cultivars. For instance, in 'Redgauntlet' and
'Talisman cultivars', trusses/crown was the most important

yield component (Guttridge and Mason, 1966; Gooding,
Jennings, and Tophan, 1975) while 'Cambridge Favourite'
had a low coefficient of variation for the number of
trusses/crown (Guttridge and Mason, 1966; Mason, 1966).

Strawberry trusses are modified stems that always
terminate a growth axis. Flower bud initiation results
when either the daily light periods are shortened
below some "critical" length or the temperature cools
(Darrow, 1966). In the northern United States, the
onset of autumn brings shortened daylengths and cooler
temperatures favorable to flower bud initiation. En-
vironment, nutrition, genetics, and the size of the
plant can affect the development of inflorescences
(Guttridge, 1955). Controlled environment trials with
container grown strawberry plants have shown that fruit
truss induction and vegetative growth are negatively
related (Borthwick and Parker, 1952; Guttridge, 1960).
A decrease in the number of trusses/crown was noted for
Redgauntlet in Scotland as the size of the plant in-
creased (Guttridge and Anderson, 1974). A field study
in Scotland (Guttridge and Anderson, 1973), showed
that with increasing plant size there was a reduction
in the number of flower trusses, some crowns being
barren of fruit the following summer. It was concluded
that flower truss initiation is more likely to fail in

large than small plants, but factors other than plant
size may also play an important role. Mason (1966)
suggests that a tendency toward barrenness is related
to a cultivar's sensitivity to photoperiodic induction
of the flower trusses, with the less sensitive geno-
types displaying more barrenness. Hughes (1972)
noted greater truss deficiencies in higher than in lower
latitudes (e.g., Scotland vs. England).

Way and White (1968) showed that while high nitro-
gen levels failed to reduce the number of trusses/crown,
yield decreased through either poor fruit set or fewer
flowers per inflorescence. Commonly, less than 80% of
the flowers per plant actually set fruit (Kroneberg,
Braak, and Zeilinga, 1959; Kroneberg, 1959; Waister,
1979; Webb, Purves, White, and Ellis, 1973). Flower
abortion, reduced fruit set and malformation of fruit
have been associated with poor pollination, fertiliza-
tion and/or receptacle development (Kroneberg, 1959;
Kroneberg, Braak, and Zeilinga, 1959; Thompson, 1971).
Temperature conditions greatly affect the length of
time between fertilization and fruit maturity. Generally,
30 days is thought to be the average time span of this
process, but as few as 20 days under ideal conditions
may be needed (Darrow, 1966).

After fertilization of the ovule, production of growth stimulants cause enlargement of the receptacle tissue in the area near the developing achene (Nitsch, 1950). The strawberry achene is actually a single seeded fruit (Winston, 1902). The number of ovules per berry is set during the flower bud differentiation stage, which occurs in the fall for spring fruiting varieties. According to Havis (1943), the growth of the strawberry fruit after fertilization is principally by increase in cell size and enlargement of intercellular spaces with very little cell division. Knee et al. (1977) showed that cell division in strawberry fruit ceases about 7 days after petal fall.

Janick and Eggart (1968) showed that fruit size in strawberry was influenced by position of the fruit on the inflorescence, the number of achenes that develop on the berry surface, competition between fruits on the inflorescence and general plant vigor. It has been shown that the primary flower may have 400 or more pistils, compared with 200-300 for secondaries and 50-150 for tertiary flowers (Janick and Eggert, 1968; Valleau, 1918). Significant correlations were found between achene number and fruit weight. Also, larger secondary fruits were obtained when the primaries were removed, giving credence to the existence of competition within the inflorescence. However, berries on

basal-branched inflorescences average larger fruit at all ranks compared to high branching trusses, with the secondary berries on basal branched trusses being 91% of the weight of the primaries (Darrow, 1929).

The extent to which growth substances are produced by the achenes and their effects on the receptacle tissue determines the amount of berry expansion. Abbott et al. (1970) expressed the degree to which berries expanded in terms of the number of achenes per unit of fruit surface by counting the achenes visible in a circular aperture of 1 cm^2 placed on the berry surface. As the fruit swell, the number of achenes/cm^2 declines. The lowest value reported is about 6 per cm^2 but Webb et al. (1974) adopted 8 achenes per cm^2 as a practical level indicative of maximum berry expansion under field conditions. Quantification of the extent of berry expansion via achenes/cm^2 makes it possible to determine the ratio of actual yield to potential yield. Lack of berry enlargement may be due to insufficient water supply. However, Webb et al. (1974) used a water culture system in their strawberry size experiments wherein the roots were immersed in well aerated water. Certainly, access to water was not limiting, and yet, berries failed to enlarge to their potential. From this we infer

that other factors besides water supply should be investigated as influences affecting berry expansion. For instance, a limiting water transport system would inhibit berry expansion.

Plant size is an important parameter to measure in assessing yield potential of strawberry genotypes (Guttridge and Anderson, 1981). Lacey (1973) found plant size in autumn to be positively correlated with the following year's yield. Larger plants have been found to produce more flowers (Morrow and Darrow, 1940; Rogers and Edgar, 1938), and greater yields than smaller plants (Peacock, 1939; Rogers, 1931). However, Guttridge and Anderson (1973) found that in one field, an increase in plant size gave a steep increase in yield, while another field showed only a moderate increase in yield with increasing plant size.

The leaf canopy is the major region of photo-synthate production in the strawberry plant. The number of leaves and leaf area in the fall have been positively correlated with fruit production the following year (Sproat et al. 1935). Jahn and Dana (1970b) found that plants that had the largest leaf area early in the season continued to grow more rapidly than those with less leaf area.

Quantitative Analysis of Plant Growth

The importance of measuring the biological efficiency of crop plants was recognized early in this century. Blackman (1919) provided much of the basis for the quantitative analysis of plant growth. He proposed that if: 1) the rate of assimilation per unit area and the rate of respiration per unit plant mass remained constant; and 2) the size of the leaf system bore a constant relationship to the dry weight of the whole plant, then the rate of production of new plant material would be proportional to the size of the plant. He described this as being analogous to the compound interest law wherein the amount of interest earned on money deposited in a bank would increase as the amount of money in the account increased. He termed the rate of interest the "effiency index of production". Briggs, Kidd, and West (1920) rebutted Blackman's theory stating that separate estimates of growth rate should be made throughout the course of growth, because the rate of growth would change. They suggested the term 'relative growth rate' be used to replace 'efficiency index', which has an implication of constancy in growth rate.

Attempts to correlate the leaf area with the dry weight of a plant gave birth to the term 'unit leaf rate' (Briggs, Kidd, and West, 1920). They defined this term as the mean rate of dry weight increase per unit leaf area. Gregory (1926) later coined the term 'net assimilation rate' for the same measure. The latter term has been used widely since its adoption. However, Evans (1972) states a convincing argument for the re-adoption of 'unit leaf rate' and the author of a recent monograph on plant growth analysis affirms his commitment to the use of unit leaf rate (Hunt, 1982).

This early work by Blackman (1919) Briggs, Kidd, and West (1920) and Gregory (1926) laid the foundations of what came to be known as the classical approach to plant growth analysis. Generally, the classical approach involves the calculation of mean rates of change in growth parameters taken from relatively few harvests at extended intervals during a growth period.

Reed and Holland (1919), and Robertson (1923) attempted fitting their growth data to a logistic (or autocatalytic) function. The theory employed was that the growth rate of the plant was controlled by a single autocatalytic chemical reaction. This gross over-simplification of the complex plant growth

process and a lack of sufficient computing power to
allow for non-linear regression analysis served to
undermine this early work. With the development
and utilization of computer technology, handling
of plant growth analysis data became more
practical.

In contrast to the classical approach to plant
growth analysis, the functional approach fits mathe-
matical functions to the primary data (e.g. plant
dry weight vs. time, and leaf area vs. time), and
in this way, describe the growth trends of these
variables in relation to time. Then, fitted values of
data are extracted from these primary growth curves
and used to obtain instantaneous values of various
derived quantities. The advantages of this approach
have been discussed by many authors, including Radford
(1967) and, more recently, Hunt (1979). Among the
advantages are: 1) information from all sampling
occasions is used in determining each value of the
derived quanties; 2) small deviations from the
overall trend may be smoothed to gain an impression
of growth which is free from random fluctuations;
3) many of the assumptions involved in the calculation
of mean values of quanties such as unit leaf rate
(Coombe, 1960; Evans and Hughes, 1962; Whitehead and

Myerscough, 1962; Evans 1972, p. 268) and leaf area ratio (Ondok, 1971) are avoided, leaving the only essential assumption being that the fitted growth functions adequately describe the primary data.

Comparisons of the classical and functional approaches to handling plant growth data have been performed by Sivakumar and Shaw (1978) on soybean; Hammerton and Stone (1966) on pale persicaria; Buttery (1969) on soybean; Eckhardt et al. (1971) on sunflower; Silsbury (1971) on perennial ryegrass; Buttery and Buzzell (1974) on soybean; Hunt and Parsons (1977) on maize; Hurd (1977) on tomato; Hunt and Evans (1980) on maize; Causton and Venus (1981) on wheat, maize, sunflower and birch; Parsons and Hunt (1981) on corn.

In selecting the technique and model for describing plant growth trends, one must give equal consideration to: 1) statistical precision; and 2) what Hurd (1977) labeled "biological expectation". Each must temper the other and be strongly attuned to reality. It matters not how exactly the mathematical function fits the primary data if the resulting curve has no basis in biological reality.

YIELD COMPONENT ANALYSIS OF

'BENTON' AND 'OR-US 4356' STRAWBERRIES

ABSTRACT

Yield component analysis of 'Benton', Oregon's leading cultivar and an advanced breeding selection, 'OR-US 4356', was conducted during the first (1981) and second (1982) fruiting years. 'Benton' produced 25-30% more crowns/plant than 'OR-US 4356'. 'Benton' had fewer trusses/crown in 1981 (0.93 vs. 1.47) and equal figures in 1982 (1.5). 'OR-US 4356' had about 60% higher numbers of fruit/truss in each season. However, 'Benton' averaged 75% greater mean berry weight than 'OR-US 4356' so that in each season the two genotypes produced essentially the same yields/plant, averaging 0.82 kg in 1981 and 0.94 kg in 1982. There was no significant difference in total achenes/berry between genotypes (averaged 202 in 1981 and 239 in 1982). Linear regressions of berry weight versus achenes/berry were significantly different between genotypes in each season. 'Benton' had less achenes/gram of berry (24 vs. 34) and achenes/cm^2 (10.6 vs. 14.0). 'OR-US 4356' fell short of its yield potential due to its inability to reach maximum berry expansion.

INTRODUCTION

Analysis of the components of strawberry yield can be used to evaluate genotypes, identifying strengths or weaknesses in the balance of their components. Yield per strawberry plant can be attributed to the multiplicative effects of four yield components: 1) the number of crowns/plant, 2) number of trusses (inflorescences)/crown, 3) number of berries/truss and 4) mean berry weight (Hondelmann, 1965; Webb, Purves, White and Ellis, 1974).

The degree of berry expansion is a useful paramater in assessing yield potential. The number of achenes per unit area of berry surface is used to quantify the extent of berry expansion. Lower values represent greater berry swelling. Webb, et al. (1974) adopted 8 achenes/cm^2 as a practical level indicative of maximum berry expansion under field conditions.

To quantify yield characteristics of field grown strawberries in Oregon, a yield component analysis of two strawberry genotypes was begun. 'Benton', Oregon's leading cultivar, and an advanced breeding selection, 'OR-US 4356', were chosen for the study because of their apparent contrast in growth and fruiting habits.

MATERIALS AND METHODS

Planting occurred in mid-May, 1980, on a
Willamette silt loam soil at the North Willamette
Experiment Station near Aurora, Oregon. Plants were
set 38 cm apart in rows separated by 1.0 m. Fertilizer
(10-9-8 NPK, 336 kg/ha) was applied in June, after
plant establishment, and again in August the following
year during renovation and after runner removal.

On June 15 in each year, which was during the
first part of fruit harvest, 25 randomly selected
plants of each cultivar were destructively harvested
to determine the numbers of crowns/plant, trusses/
crown and fruits/truss. An additional 25 plants/
cultivar were selected and their fruit harvested
as it ripened over the course of the season.
Harvested fruit from each plant was used to obtain
total yield and mean berry weight. A subsample
was stored in a freezer for later determination of
total achenes/fruit and achenes/cm^2. Achenes/cm^2
was obtained by averaging the number of achenes
visible within a circular 1 cm^2 aperture held against
the berry surface at two locations (Abbott et al.,
1970). After final harvest in the second year, the
leaf area of plants used in yield determinations was
measured using an electronic leaf area meter.

RESULTS AND DISCUSSION

'Benton' and 'OR-US 4356' produced yields/plant that were not significantly different in either fruiting year (Table 1), averaging 21,300 kg/ha for 1981 and 24,000 kg/ha for 1982. However, the two genotypes achieved their yields with a decidedly different composition of yield components.

'Benton' produced 25-30% more crowns/plant than 'OR-US 4356' in each year (Table 1). Several investigators have documented increased yields with increasing crown numbers on a per hectare basis (Rogers and Moblibowska, 1951; Anderson and Guttridge, 1976; Christopher and Shutak, 1938; Craig and Aalders, 1966; Craig, Aalders and Leefe, 1973; Hondelmann, 1965). However, insofar as assessing fruiting characteristics of a strawberry clone is concerned, Guttridge and Anderson (1981) conclude that crown numbers are not the most reliable guide. They state that individual plant records of trusses/crown or plant, fruit/truss, mean berry weight, and some measure of plant size (not crown numbers), is necessary to assess the yield characteristics and potential of a strawberry genotype.

'Benton' averaged less than one (0.93) truss/ crown in its first fruiting year, whereas 'OR-US 4356' produced nearly 1.5 trusses/crown (Table 1). Obviously, some of Benton's first year crowns were barren. Breen and Martin (1981) also observed that 'Benton' produced less than one truss/crown in its first fruiting year. By the second year, 'Benton' showed less barrenness and each genotype averaged 1.5 trusses/crown. Mason (1966) suggests that a tendency toward barrenness is related to a genotype's sensitivity to photoperiodic induction of the flower trusses with less sensitivity causing more barren- ness. Perhaps a genotype's sensitivity to this process may change with age, thus helping to explain 'Benton's' first, but not second year barrenness.

'OR-US 4356' produced significantly higher numbers of fruit/truss than 'Benton' (Table 1). This was true for single and double truss crowns in the first and second fruiting years (Table 2). 'OR-US 4356' had 100% and 37% higher numbers of fruit/plant than 'Benton' in the first and second fruiting years respectively. Mean berry weight was higher in 'Benton' than 'OR-US 4356' in each season (Table 1). By producing larger fruit, 'Benton' was able to achieve yields equal to 'OR-US 4356'.

Similar compensatory effects of strawberry yield
components have been reported (Guttridge and Anderson,
1973).

Berry size depends on plant performance in three
separate stages of development: 1) during flower
formation in the fall, the number of ovules created
on the receptacle is determined; 2) in the spring,
the efficiency of fertilization of those ovules is
determined; 3) between pollination and ripeness,
the amount of tissue which develops along with each
achene is determined (Abbott et al., 1970 and
Webb et al., 1974). The total number of achenes
per berry represents the number of ovules formed on
the flower. Achene numbers per berry vary within
the inflorescence according to berry rank, with the
primary fruits having the most (Janick and Eggert,
1968; Valleau, 1918).

The difference in berry size between 'Benton'
and 'OR-US 4356' cannot be attributed to achene
numbers as there was no significant difference in
achenes per berry in either year (Table 3). This
fact, coupled with 'Benton's' higher mean berry
weight, explains the significantly greater number of
achenes/gram of berry for 'OR-US 4356' (Table 3).
Both genotypes show a linear increase in berry

weight as the number of achenes per berry increases (Fig. 1). However, the two regression lines are significantly different at the 1% level, with 'OR-US 4356' producing less berry weight than 'Benton' with equal numbers of achenes.

Abbott et al. (1970) expressed the extent of berry expansion in terms of the number of achenes/ cm^2. The lowest achenes/cm^2 values recorded in this study were 6 and 8.5 for 'Benton' and 'OR-US 4356' respectively. Webb et al. (1974) adopted 8 achenes/ cm^2 as a practical level indicative of maximum berry expansion in field plantings. 'OR-US 4356' achieved 59% of this standard level of berry expansion in the first year and 55% for its second fruiting year (Table 3). This contrasts with 'Benton', which attained 83% and 69% of the maximum level of berry swelling for the first and second fruiting years respectively. 'Benton' maintained a lower achene density than 'OR-US 4356' throughout the first and second fruiting seasons (Fig. 2; also see Fig. 8 in Appendix). The trend for both genotypes was an increasing achene density accompanied by a decreasing mean berry weight as the fruiting season progressed. The decline in fruit weight was much greater than the increase in achenes/cm^2 due to a

decrease in berry ranking being harvested. 'Benton' maintained a stable level of achenes/cm^2 in its first year (8-12 achenes/cm^2), indicating that even smaller berries of decreased rank are able to attain near maximum levels of berry swelling (Figure 2). Increases from 10-12 achenes/cm^2 occurred after about July 8, when berries were about 5g. This is near the time commercial growers stop harvesting.

The leaf canopy produces photosynthates that are partitioned to its various plant parts. Leaf areas of 'Benton' and 'OR-US 4356', measured at the end of fruit harvest in the second fruiting year were both about 0.42m^2. Strawberry genotypes vary in their ability to partition photosynthate to their fruit (Guttridge and Anderson, 1981). The failure of 'OR-US 4356' to size up its fruit could be due to: 1) insufficient photosynthate to support the large number of fruit/truss; 2) fruit compete weakly for whatever level of photosynthate is available; 3) the genotypes's photosynthate and/or water transport system is limiting; 4) the auxin activity of its achenes is not great enough to stimulate receptacle development necessary for maximum berry swelling; 5) the receptacle tissue's sensitivity to auxin is limiting.

Abbott, et al. (1970) suggest that because at each successive stage of inflorescence branching there is a decrease in potential berry size, the most efficient use of available achenes would arise with an increased number of inflorescences per plant, each having fewer flowers. This appears to be the pattern of development with 'Benton' as it sets fewer fruit/truss (5-6 vs. 8-9 for 'OR-US 4356') while producing sufficient trusses/plant to achieve satisfactory yields.

Table 1. Mean values of yield components for 'Benton' and 'OR-US 4356'.

	1981		1982	
	'Benton'	'OR-US 4356'	'Benton'	'OR-US 4356'
Crowns/plant	11.40	8.76**[z]	15.68	12.48*
Trusses/crown	.93	1.47**	1.53	1.54
Number of fruit/truss	5.72	9.01**	4.69	7.90**
Mean berry wt. (g)	11.11	5.84	7.63	4.76**
Total yield/plant (g)	811.93	832.77	929.32	952.31

[z]Significant at 5% (*) or 1% (**).

Table 2.   Number of fruit/truss on single and double truss crowns of
           'Benton' and 'OR-US 4356' for their first (1981) and second (1982)
           fruiting years.z

	1981		1982	
	'Benton'	'OR-US 4356'	'Benton'	'OR-US 4356'
Single truss crowns	5.54	9.10***y	4.46	8.30***
Double truss crowns	5.20	8.82***	5.04	7.99***

zMean values of fruit/truss were recorded from the destructive harvest
 of 25 plants/genotypes in mid-June of both years.

ySignificant difference between cultivars at 0.1%.

Table 3. A comparison of achenes for 'Benton' and 'OR-US 4356' in relation to berry weight and fruit surface.

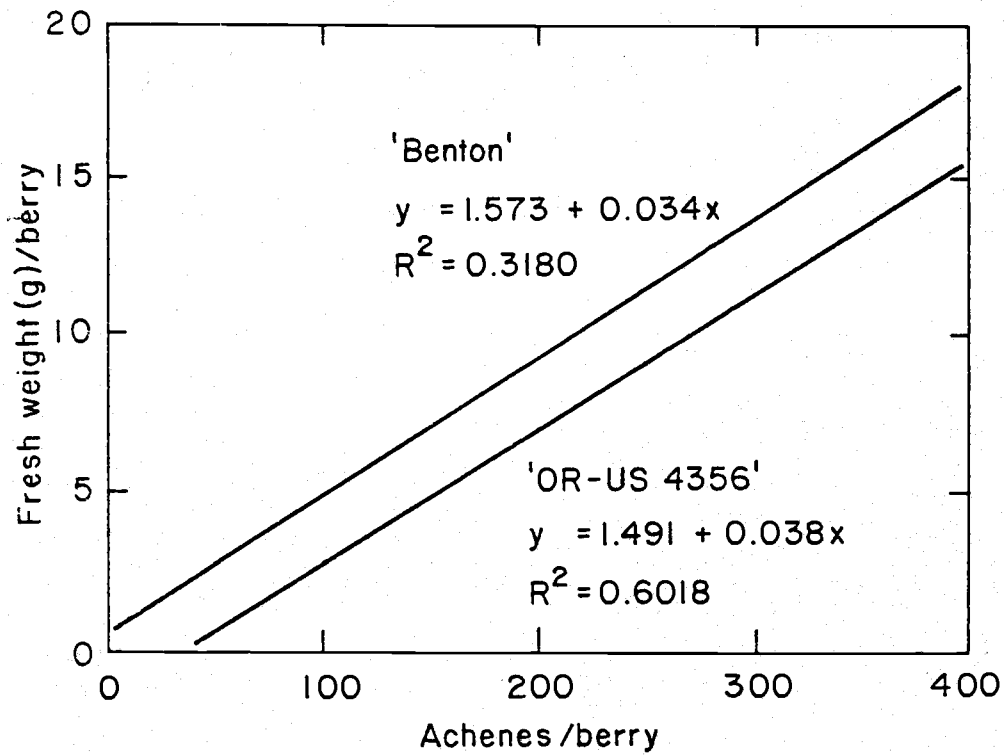|	1981		1982	
	'Benton'	'OR-US 4356'	'Benton'	'OR-US 4356'
Total achenes/berry	217.17	186.21	238.63	239.60
Achenes/g fresh wt.	21.58	32.79**z	26.53	36.13**
Achenes/cm^2	9.64	13.51**	11.56	14.53**

zSignificant at 1%

Figure 1. Regression analysis of berry weight
vs. achenes/berry for 'Benton' and 'OR-US 4356'
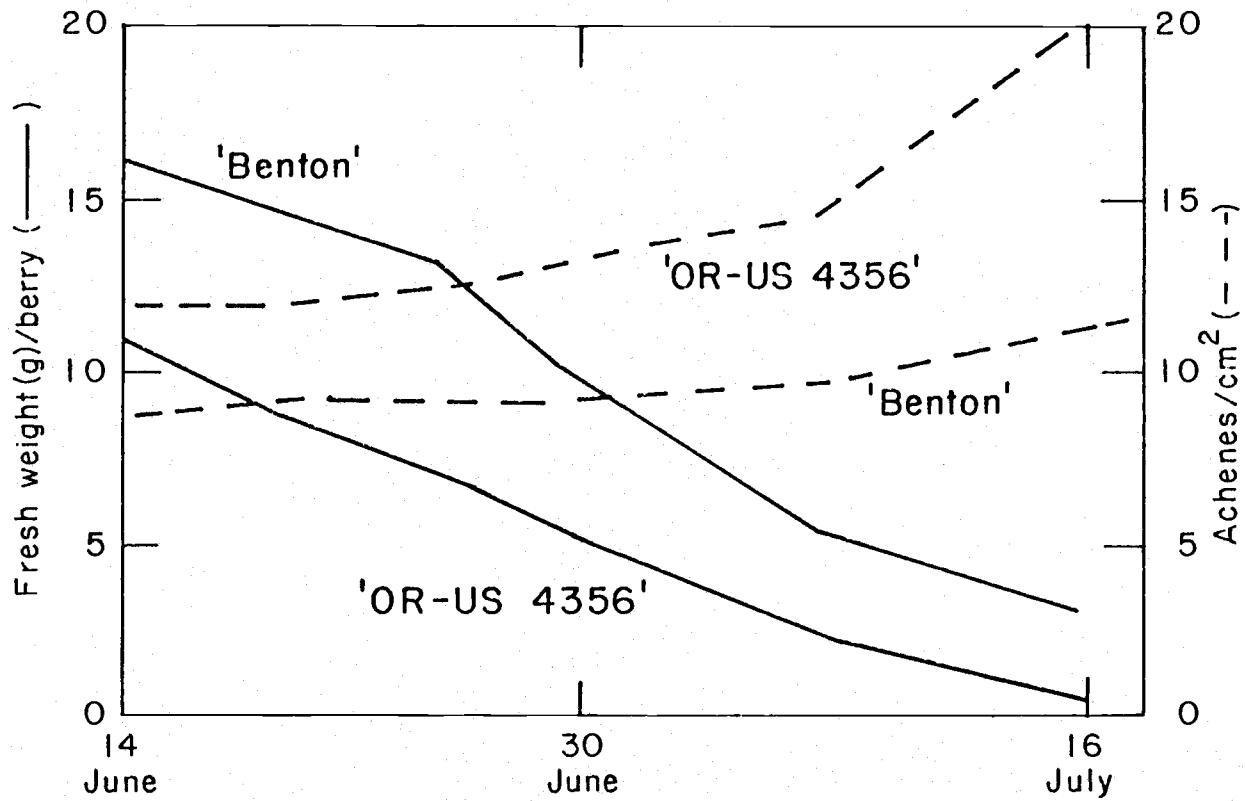strawberries in 1982.

Figure 2. Change in mean berry fresh weight (g/berry) and achene density (achenes/cm²) for the first fruiting year (1981).

FUNCTIONAL GROWTH ANALYSIS OF

FIELD GROWN STRAWBERRY

ABSTRACT

Frequent sampling and functional growth
analysis were used to quantify growth of field
grown strawberry plants ('OR-US 4681') during the
summer of establishment and through flowering and
fruiting the next spring. Plant dry weight and
leaf area increased rapidly during mid-summer,
but thereafter gains slowed and finally ceased in
October. This was reflected in the absolute growth
rate (AGR) which peaked at 1 g dry matter/day
near September 1, then fell to zero by early
October. Over this period, weekly mean temperature,
solar radiation, and daylength decreased by 37%,
47% and 35% respectively. Relative growth rate
(RGR) declined steadily from a high of 44 mg/g/day
at the end of June. Unit leaf rate (ULR) showed a
similar pattern, starting at 9 $g/m^2/day$. During the
following April through June, both plant dry weight
and leaf area increased at exponential rates. The
growth environment improved throughout this period
and the AGR increased continuously but RGR remained
constant at 19 mg/g/day. The rate of dry matter
accumulation in fruit was exponential, whereas that
in leaf lamina and stems (crowns plus petioles)

showed linear increases. Because of fruiting,
a much smaller proportion of dry matter was par-
titioned to leaves than during plant establishment.
However, ULR rose from 5.5 to 6.5 $g/m^2/day$,
indicating that dry matter production was relatively
constant during flower and fruit production.

INTRODUCTION

Investigation of the growth relationships in
the strawberry plant have revealed high correlations
between initial plant weight and plant age, leaf
production rate and early leaf area (Jahn and
Dana, 1970). Larger plants were observed to produce
more flowers and greater yields than smaller
plants (Morrow and Darrow, 1940; Peacock, 1939;
Rogers, 1931; Rogers and Edgar, 1938). The leaf
area and number of leaves per plant in the fall has
been positively correlated with fruit production
the following year (Sproat, et al., 1935). Studies
such as these generally involve the correlation of
one stage of plant development with another stage
separated by weeks or months. Quantification of
the growth trends of the strawberry plant continuously
over extended periods of time have been lacking.

The purpose of this study was to quantify
the production and allocation of dry matter in
the strawberry plant during its establishment and
first fruiting years. Frequent destructive
harvests of whole plants and the use of functional
growth analysis techniques (Hunt, 1982; Causten and

Venus, 1981) provided an effective means to model strawberry plant growth before and during flower initiation, flowering and fruiting.

MATERIALS AND METHODS

Certified nursery plants of 'OR-US 4681',
an advanced breeding selection, were planted
May 11, 1981 in rows at 0.38 m x 1.0 m spacing on
Willamette sandy shot loam soil at the North
Willamette Experiment Station near Aurora, Oregon.
Standard pest control practices were employed and
the crop was irrigated as needed. The study was
divided into two phases: 1) the establishment year
and 2) the first fruiting year. Flowers and fruit
were not removed from the plants during establish-
ment. In order to simulate commercial strawberry
production conditions, the plants utilized in the
first fruiting phase had their runners removed
in August, 1981, and received an application of
336 kg/ha of 10-9-8 NPK.

Starting on June 27, 47 days from planting,
3 plants were dug every 3-4 days until October 28.
Sampling was again initiated on April 15, 1982 of
the first fruiting year and continued until after
the commercial harvest period at the end of June.
Runner plants were not included in the plant
samples. Mother plants were dug, washed and
dissected into roots, fruits, green leaf laminia

and stems (which included crowns, petioles and trusses), oven dried, and weighed. Leaf area per plant was estimated by dividing total leaf dry weight by the mean specific leaf weight which was determined from the weight of 10 dried leaf discs (each 2.0 cm^2) punched from representative leaves. On 6 occasions, evenly spaced over the course of the study, leaf area per plant computed via the above method was compared to that obtained using an electronic leaf area meter. Using 6 plants per comparison, the two methods agreed within ± 5%. Temperature and solar radiation were recorded at the site.

Logarithmic transformations (natural log) of primary data (plant dry weight, leaf area, and fruit dry weight) were made, rendering the variability more nearly homogeneous over time. Following Hunt (1982), the transformed data were fitted to the empirical functions:

$$W = \exp[f_W(T)]$$
$$L = \exp[f_L(T)]$$

where W is plant dry weight, L is leaf area per plant and T is time. Transformed data were used to calculate growth parameters as follows (Hunt, 1982):

Relative growth rate (RGR) $= \frac{1}{W} \cdot \frac{dW}{dT} = f'_W(T)$

Absolute growth rate (AGR) $= \frac{dW}{dT} = f'_W(T) \cdot \exp[f_W(T)]$

Leaf area ratio (LAR) $= L/W = \exp[f_L(T) - f_W(T)]$

Unit leaf rate (ULR) $=$

$\frac{1}{L} \cdot \frac{dW}{dT} = f'_W(T) \cdot \exp[f_W(T) - f_L(T)]$

ULR is equivilent to the term net assimilation

rate (NAR) used by some authors.

The regression equations used were chosen

with the intent of balancing statistical exactitude

and biological realism. For the primary data of

plant dry weight and leaf area in the establishment

year (see Table 4) the quadratic term in the third

order polynomial was dropped from the model because .

it did not add significantly to the model.

RESULTS

Establishment Year

Plant dry weight and leaf area as functions
of time showed an exponential phase of growth for
about 5-6 weeks after plant sampling was initiated
(Fig. 3A, Table 4). The accumulation of dry matter
and leaf area then slowed with the onset of cooler
autumn temperatures, shortening daylength and
declining solar radiation (Fig. 4). This decrease
in plant growth is more clearly seen in the rapid
decline of the AGR from a peak of 1 g/day in early
September to zero by early October. During this
period, temperature, solar radiation and daylength
fell by 37%, 47% and 35% respectively.

Fig. 5A shows that the plant partitioned
nearly equal portions of dry matter into leaf
lamina and stems (included the crowns and petioles).
The flowers were not removed in the establishment
year and fruit dry weight per plant was approximately
1-2 g early in the season (data not shown). The
dry weight of recovered roots increased slightly
as plants became established.

RGR and ULR showed curvelinear declines from
maximum values at the start of sampling in late
June (Fig. 3B). The initial values were

44 mg/g/day (RGR) and 9 g/m^2/day (ULR), but by October, negative values were obtained. However, LAR, the ratio of leaf area to plant dry weight, increased 27% during the sampling period, most of the gain occurring from late August to October.

First Fruiting Year

The natural logarithms of plant or fruit dry weight or leaf area as functions of time in the fruiting year all fit linear equations (Fig. 6A, 6C, and Table 4), indicating that these parameters increased at an exponential rate. The AGR of the whole plant increased from 1 g/day in mid-April to 3.5 g/day in June (Fig. 6A). Whole plant RGR was constant at 19 mg/g/day throughout the 75 day sampling period. The LAR declined 15% while the ULR increased 18% over this period (Fig. 6B). In contrast to the similar dry matter allocation of leaves and "stems" in the establishment year (Fig 5A), the structural portions of the plant ("stems") contained over 70% more dry matter than the leaves in the first fruiting year (Fig. 5B). This smaller partitioning of dry matter to leaves is further reflected in lower LAR values for the fruiting year (0.03 - 0.04 m^2/kg) compared to that in the summer of establishment (0.05 - 0.06 m^2/kg),

(Fig. 3B and 6B). The recoverable root weight remained at about 6 g. Much of the fruit growth occurred during June, with the AGR of the fruit increasing about 400% between late May to the end of harvest (Fig. 6C). The RGR for the fruit was 58 mg/g/day throughout the sampling period.

DISCUSSION

The rapid decrease in AGR (Fig. 3A), beginning
in early September, probably resulted from the
declining temperature and solar radiation which
accompanied the decrease in daylength. By late
August, the mean temperature had dropped below
18° C (Fig. 4), the temperature Heide (1977) found
optimum for dry matter production in strawberry.
Leaf production in strawberry slows in autumn and
is highly correlated with temperature (Arney, 1953).
Petiole length and lamina size are reduced both
by cool temperatures and short days (Heide, 1977).
In accord with these findings, leaf area per mother
plant reached a maximum, then leveled off in the
short photoperiod, ∼ 12 hour, and cool mean temperatures,
∼ 10°C, of autumn (Fig. 3A). The slightly slower
decline in leaf area than plant dry weight resulted
in the late season increase in LAR (Fig. 3B).
Thinner leaves, which could contribute to a higher
LAR, may have been formed from mid-September to
the end of October since specific leaf weight
decreased by about 15% in this period (data not
shown).

In contrast to the rise and subsequent fall in AGR, RGR and ULR showed curvelinear declines throughout the summer of establishment (Fig. 3B). Several factors, both ontogenetic and environmental, may have contributed to these decreases. As a young strawberry plant grows, a greater portion of the plant is composed of structural material which is essentially incapable of producing the photosynthate necessary for further dry matter production. The 18-fold increase in leaf area during the summer of establishment likely led to greater shading of lower leaves, causing less efficient photosynthesis and lower rates of dry matter production. The reduction of petiole length and leaf blade area (Heide, 1977), with shorter days and cooler temperatures of autumn, could have contributed to a greater portion of the leaves being shaded as the plant canopy enlarged.

However, if sampling had begun soon after planting, a rise in RGR and ULR would likely have been observed for a period because leaf shading would be minimal. An early season rise in RGR and/ or ULR has been observed in seedlings (Williams, 1946) and in several annual crops (Watson, 1947).

Since sampling was initiated just after the
summer solstice, the decline in RGR amd ULR might
be attributed to declining daylength and the ac-
companying lower temperatures and reduced solar
radiation. The curves for RGR, ULR and daylength
run parallel to one another. Watson (1947) observed
a peak in ULR at the summer solstice in 4 annual
crops regardless of the planting date. ULR, being
primarily a function of photosynthesis, is more
dependent on solar radiation than other environmental
factors (Kvet, et al. 1971). In a simultaneous
comparison of the growth of barley outdoors at
Ottawa and in a controlled environment, Thorne (1961)
showed that a downward ontogenetic drift in ULR was
accentuated by the decrease in good growing conditions
outdoors in late summer.

Late in the establishment year, a larger
number of older, less photosynthetically active
leaves would be present in the canopy. Darrow (1930)
reported the average life of a strawberry leaf to be
about 2 months. As the proportion of older
leaves increased, the photosynthetic productivity
of the total leaf surface would be expected to decline
without a comparable decrease in respiration.

In the first fruiting year, the whole plant
AGR increased 270% from mid-April (just prior to
flowering) to completion of fruit harvest in June
(Fig. 6A). Guttridge (1958) reported that following
winter chilling, mature strawberry plants had
increased vegetative vigor with longer petioles
and larger leaves. This stimulative effect of
chilling likely contributed to the exponential
increases in plant dry weight and leaf area in the
first fruiting year (Fig. 6A). The longer petiole
length of winter chilled plants would position
new leaves favorably for light interception and
allow a large canopy surface to develop. The
increase and maintenance of high ULR values in the
spring of fruiting may have resulted from higher
photosynthetic efficiency of the newer leaves in
the canopy. At a comparable leaf area of $0.3m^2$ and
similar daylengths, the ULR in the first fruiting
year was twice as high as in the establishment
year (Fig.3B and 6B). This increase in ULR in
the spring with a steadily improving environment
prior to the summer solstice is consistent with
the results of Watson (1947).

The downward ontogenetic drift usually found
for RGR could have been offset by improving growth
conditions in the fruiting year, thus allowing for

the constant RGR (Fig. 6B). Respirational losses
of dry matter would have been reduced due to the
cooler spring temperatures. Much of the increase
in dry matter of the whole plant is attributable
to the exponential accumulation of dry matter in
the fruit (Fig. 5B). Furthermore, the rapid rise
in fruit weight in relation to the leaves contributed
to the slight decrease in LAR (Fig. 6B). The
presence of fruit might have stimulated ULR in the
spring since Choma et al. (1982) observed that net
photosynthesis per unit leaf area of day-neutral
strawberries was 19% higher in fruiting than in
deblossomed plants.

Table 4. Regression equations of the natural logarithms of plant dry weight (g) leaf area/plant (cm^2) and fruit dry weight (g) over time for 'OR-US 4681' strawberry.[y]

Parameter	Regression equation[z]	R^2
1981, Establishment year		
Plant dry weight	$Y = -0.6822 + 0.0484X - 0.6746 \times 10^{-6}X^3$	.97
Leaf area/plant	$Y = 3.2217 + 0.0486X - 0.6277 \times 10^{-6}X^3$	.96
1982, First fruiting year		
Plant dry weight	$Y = 3.5882 + 0.0191X$	.86
Leaf area/plant	$Y = 7.1976 + 0.0162X$	.82
Fruit dry weight	$Y = 0.2983 + 0.0576X$	.93

[y]For the establishment year x = days from the May 11 planting date; for the first fruiting year year x = days from April 1, 1982.

[z]All regression equations were significant at the 1% level.

Table 5. Regression equations of the plant parts (g) of 'OR-US 4681' strawberry in the establishment and first fruiting years.[Y]

Parameter	Regression equation	R^2
1981, Establishment year		
Leaves	$Y = 43.43 - 1.71X + 0.02X^2 - 0.67 \times 10^{-4}x^3$	.92
Stems[x]	$Y = 44.53 - 1.70X + 0.02X^2 - 0.63 \times 10^{-4}x^3$	.92
Roots	$Y = -1.65 + 0.04X$	.94
1982, First fruiting year		
Leaves	$Y = 9.30 + 0.35X$	.79
Stems[x]	$Y = 17.23 + 0.55X$	.57
Roots	$Y = 6.39 + 0.03X$	.10
Fruit	$Y = -0.78 - 0.22X + 0.01X^2$	.90

[x]"Stems" includes crowns, petioles and trusses.

[Y]For the establishment year x = days from May 11 planting date; for the first fruiting year x = days from April 1, 1982.
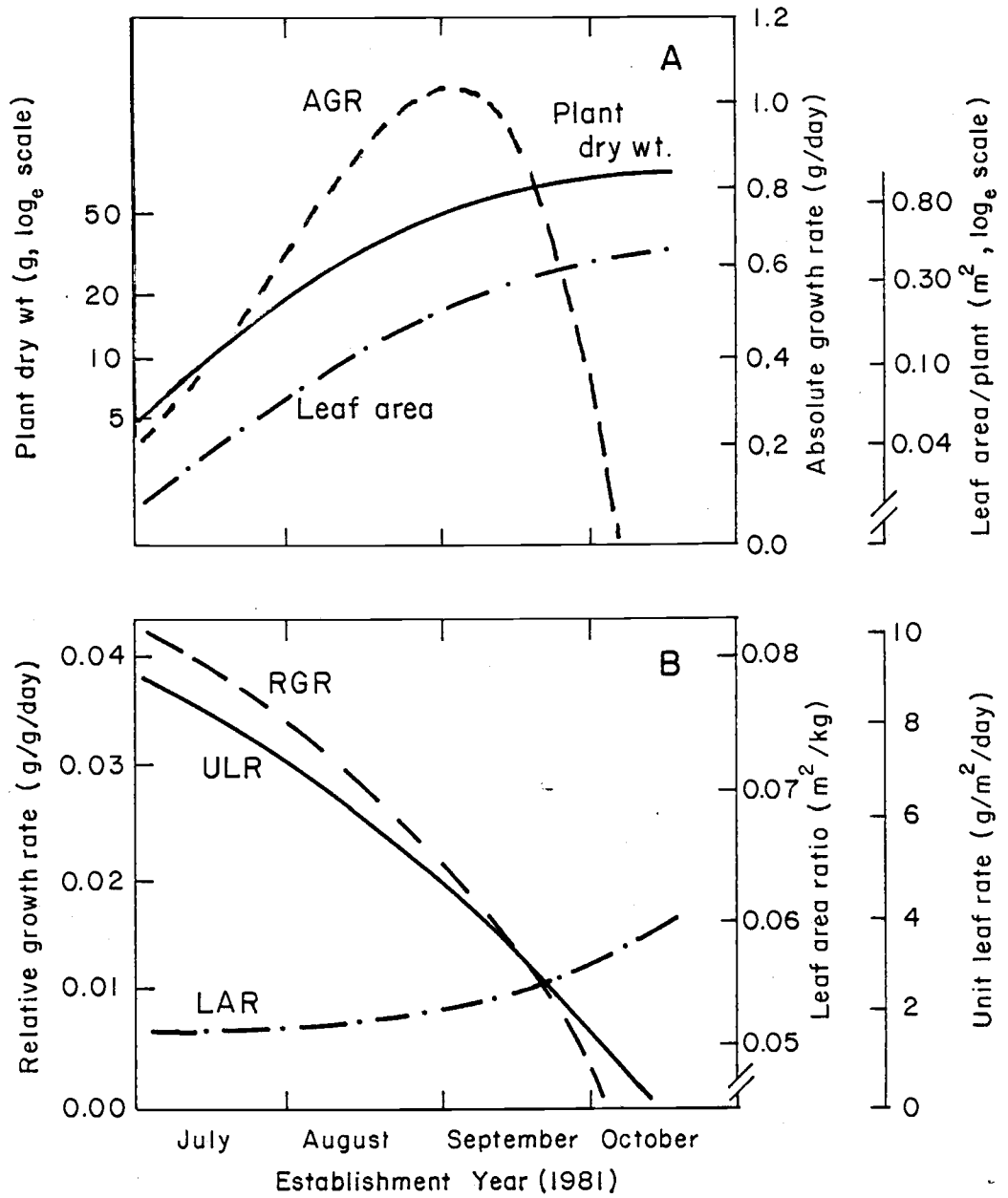
Figure 3. Change in plant dry weight, leaf area, RGR, AGR, LAR and ULR of strawberries during establishment in 1981.
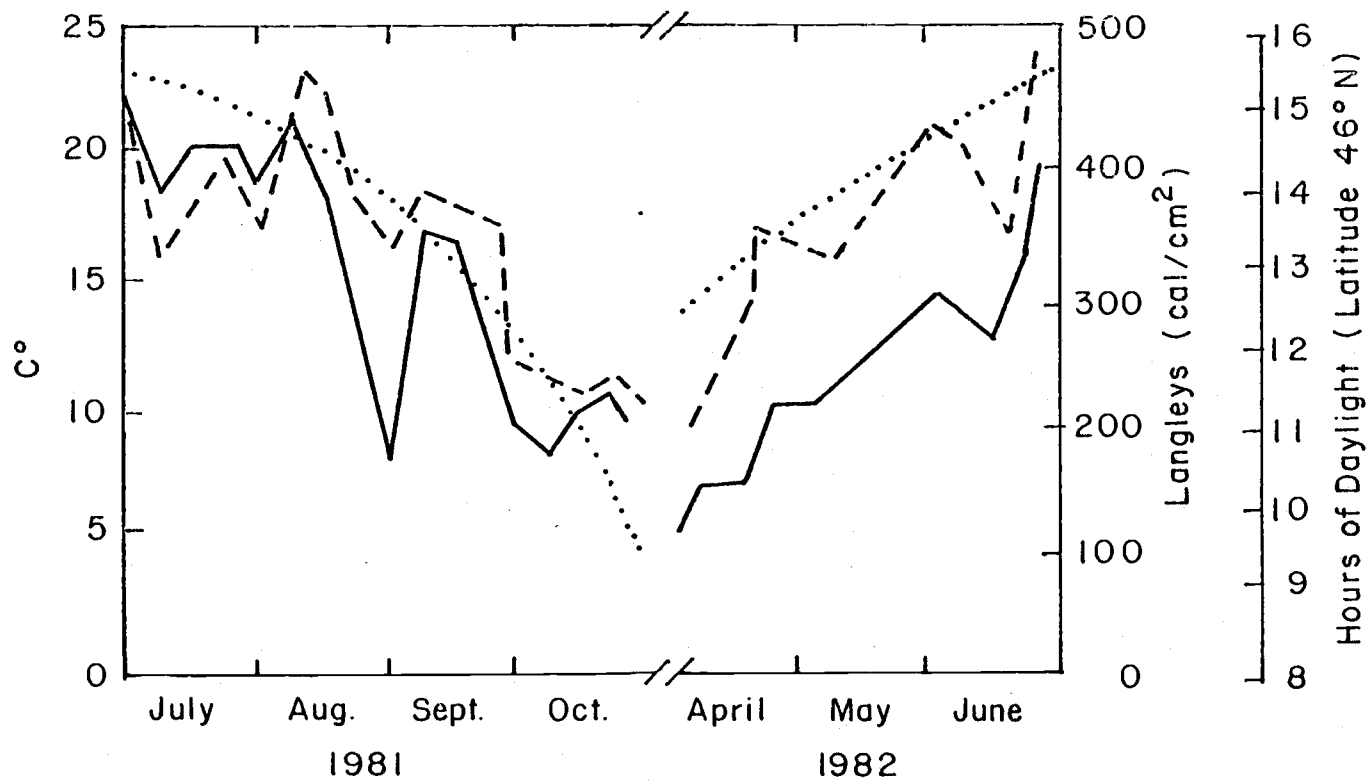
Figure 4. Weekly mean temperature (‾ ‾ ‾), solar
radiation (⸺), and hours of daylight (· · ·) for
the 1981 and 1982 growing seasons.

Sources: Oregon State University North Willamette
Experiment Station, Aurora, Oregon, for temperature
and solar radiation; Smithsonian Meterological Tables
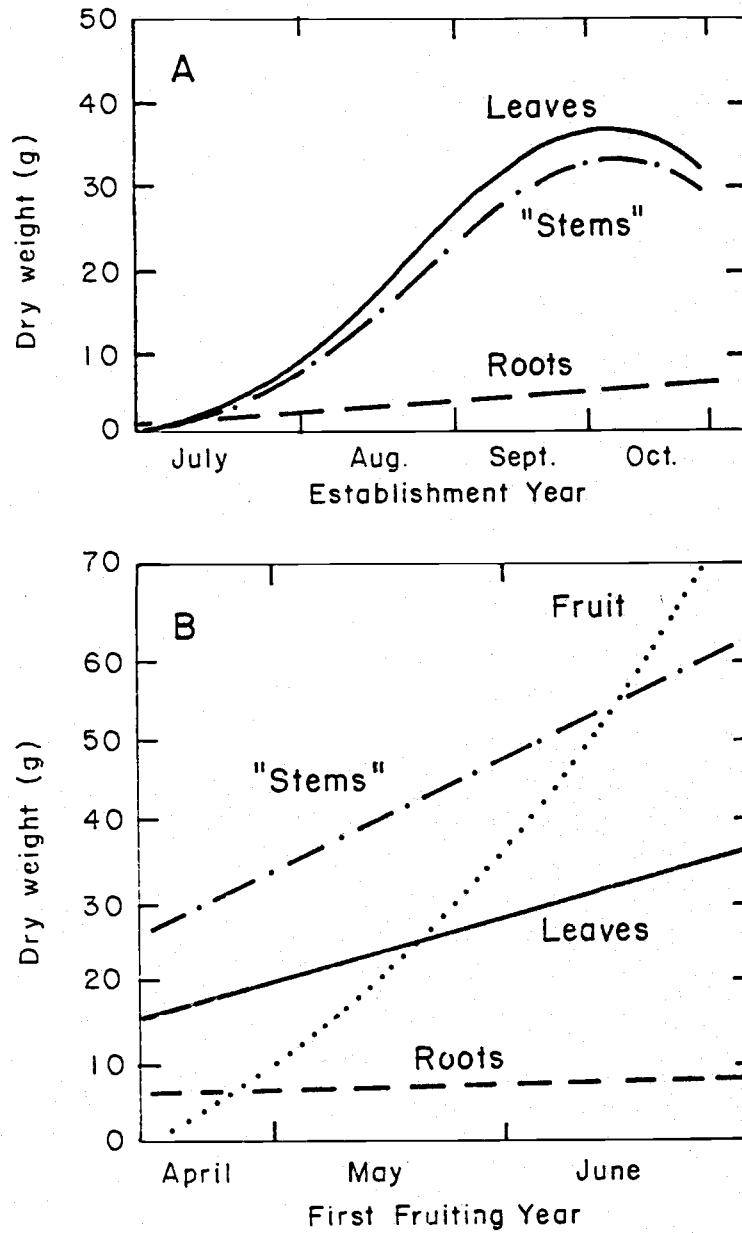for hours of daylight.

Figure 5. Dry weight of strawberry plant parts in the establishment and first fruiting years, ("stems" includes crowns, petioles and trusses).
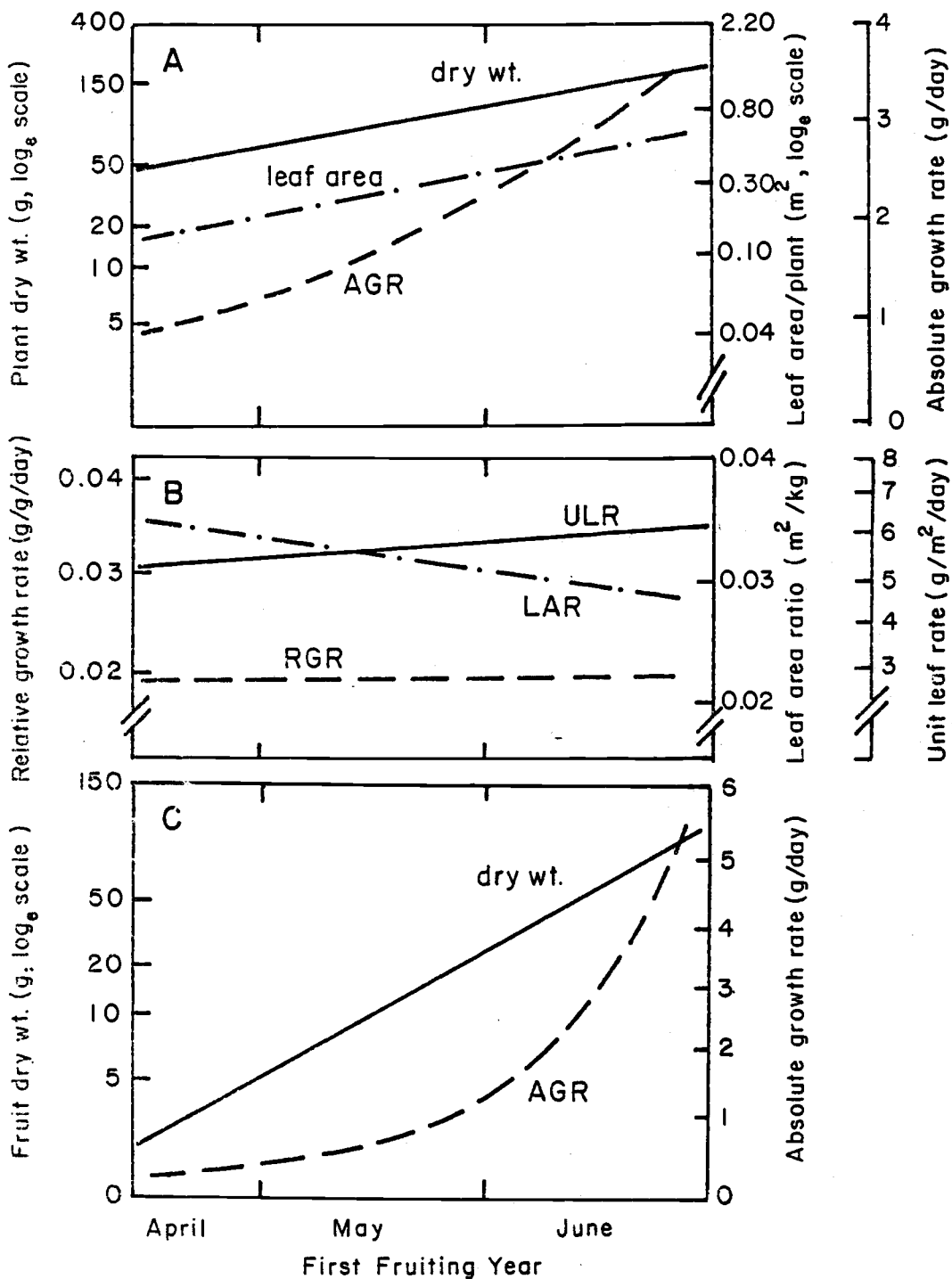
Figure 6. Change in plant dry weight, leaf area, fruit dry weight, AGR, RGR, LAR and ULR of strawberries during the first fruiting year in 1982.

CONCLUSION

The growth and development of the strawberry plant was explored using two different approaches. The analysis of the components of yield of 'Benton' and 'OR-US 4356' examined the morphological makeup of two strawberry genotypes possessing contrasting growth and fruiting habits. Although these two genotypes produced fruit yields per plant that were not significantly different, their yield components were dissimilar in many categories. 'Benton' produced fewer but larger fruit than 'OR-US 4356'. Measures of achene densities on the berry surface revealed that 'OR-US 4356' failed to attain its maximum level of berry swelling. Consequently, it failed to achieve its fruit yield potential.

In order to increase the yields of the strawberry plant, more research will be needed on the components that make up the yield in strawberries. Learning how to maximize the development of each yield component at the state in which it can be influenced would be valuable. Then, one could work to achieve a satisfactory balance of yield components that brings maximum yields for the environmental conditions in a chosen geographical area.

The functional growth analysis of 'OR-US 4681' quantified the growth trends of this advanced selection from the breeding program over the course of its establishment and first fruiting years. In the first fruiting year, the partitioning of the plant's photosynthate into the fruit resulted in the fruit containing over 40% of the plant's total dry weight. Some strawberry genotypes are weak sinks for the plant's resources, with 'OR-US 4356' being an example of this. Researchers benefit by understanding more of the mechanisms of dry matter partitioning in the strawberry plant. Once understood, one may be able to achieve methods of manipulating the plant partitioning process so as to allow for greater dry matter accumulation in the fruit, which would increase economic yields. Determination of the heritability of desirable traits in the strawberry plant, has increased the effectiveness of strawberry breeding programs worldwide. Continuation of this effort into the areas of yield component balances and efficiency of the strawberry plant's biological productivity will be valuable in improvement of crop management and plant breeding systems.

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APPENDIX

Table 6 . Fruit number/truss, fruit weight/truss and derived mean berry weight on crowns of 'Benton' and 'OR-US 4356' in their second fruiting year.^{z}

Single truss crowns	'Benton'	'OR-US 4356'
Fruit/truss	4.46	8.30***^{x}
Fruit wt. (g)/truss	19.80	37.83***
Mean berry wt. (g)^y	4.44	4.56
Number of crowns	195.00	152.00
Double truss crowns		
Fruit/truss	5.04	7.99***
Fruit wt.(g)/truss	20.17	29.89***
Mean berry wt. (g)	4.00	3.74
Number of crowns	144.00	155.00

^{x} Significant difference between cultivars at .1%.

^{y} Derived by dividing fruit/truss into fruit wt./truss. Used all fruit (ripe and unripe).

^{z} Mean values were recorded from the destructive harvest of 25 plants/ genotype in mid-June 1982.
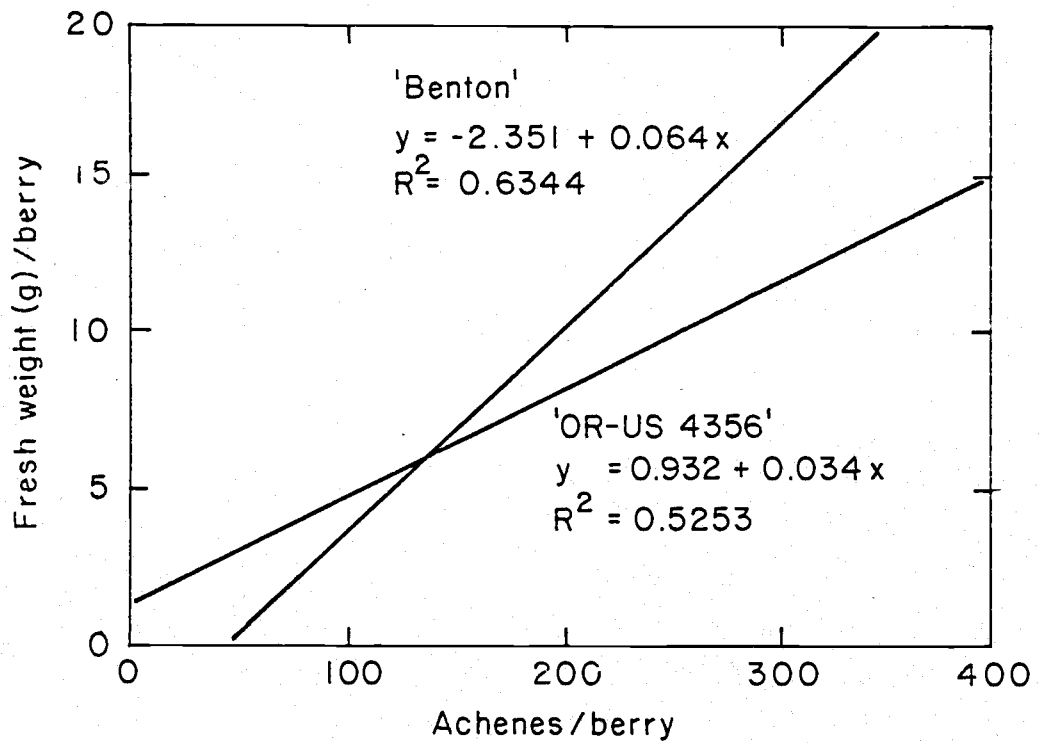
Figure 7. Regression analysis of berry weight (g) vs. achenes/berry for 'Benton' and 'OR-US 4356' strawberries in 1981.

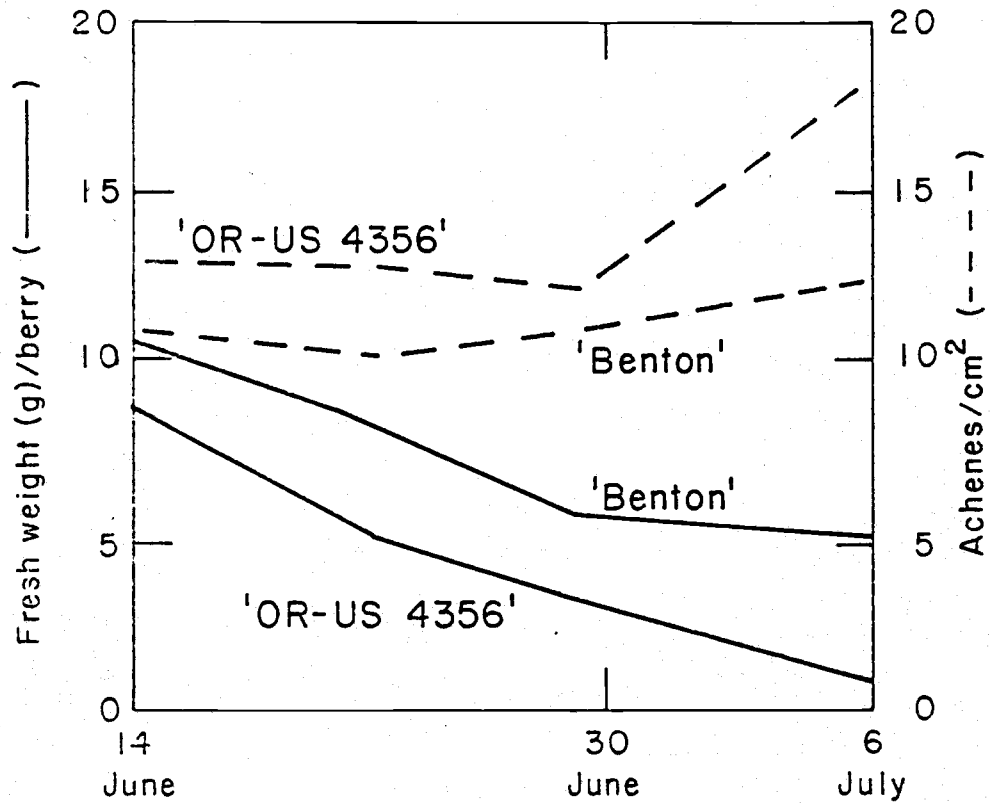The regression lines are significantly different at the 0.1% level.

Figure 8. Change in mean berry fresh weight (g/berry) and achene density (achenes/cm^2) for the second fruiting year (1982).