

AN ABSTRACT OF THE THESIS OF

Paula Mohadjer for the degree of Master of Science in Horticulture presented on September 20, 1999. Title: Nitrogen Partitioning in 'Marion' and 'Kotata' Blackberries Grown in Alternate-Year Production.

Abstract approved: _____

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Mature 'Kotata' blackberries (*Rubus* L. subspecies *Rubus* Watson) growing in the alternate year system (AY) in the field, were treated with ammonium sulfate depleted in ^{15}N in Spring, 1997. In the second year, only non-labeled ammonium sulfate was applied so redistribution could be measured. Plants were destructively sampled throughout the first and second season. 'Marion' growing in the AY system in pot culture were treated with either ammonium nitrate depleted in ^{15}N or non-labeled ammonium nitrate in the spring and/or summer of 1997 and 1998. Whole plants were destructively sampled at the end of each growing season. Total roots could not be obtained so all totals and recovery values did not include roots. In the off-year, new fertilizer N was allocated to primocanes and primocane leaves and stored N to the crown. In the on-year, new fertilizer N was allocated to primocanes, primocane leaves, and fruit and stored N to floricanes and crowns. Total dry weight and N uptake were greater in the on-year than in the off-year. 'Kotata' recovered 45% or 30% of the applied ^{15}N by the end of the first season in on- and off-year plants, respectively. 'Kotata' took up 16.5 or 25.1 $\text{kg}\cdot\text{ha}^{-1}$ N in off- and on-year plants, respectively. 'Marion' plants recovered less ^{15}N , averaging 17%. By the end of two seasons, only 19% and 8% of the applied ^{15}N was retained in on- and off-year 'Kotata', respectively, much more than the 1% retained by the potted 'Marions'. Pruning of floricanes and primocanes in October for AY production removed 73% of the N and 83% of the nitrogen derived from fertilizer (NDFF). Fruit contained an average of 38% of the ^{15}N acquired by the plant. Plants fertilized in both the on- and off-years had significantly

more dry weight, N content, and yield than plants fertilized in only one year. In 'Marion', on-year plants that received N in the previous August had a higher total dry weight, N, and NDFF than those that received no N in August.

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Nitrogen Partitioning in 'Marion' and 'Kotata' Blackberries
Grown in Alternate-Year Production.

by

Paula Mohadjer

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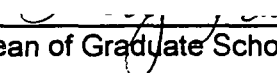
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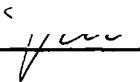


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To my Father

Nitrogen Partitioning in 'Marion' and 'Kotata' Blackberries Grown in Alternate-Year Production.

CHAPTER 1: INTRODUCTION

Oregon is the leading blackberry producer in the world with over 2755 hectares of trailing blackberries grown (Anonymous, 1998). Approximately 95% of the blackberries grown in Oregon are trailing, such as 'Marion' and 'Kotata' (Strik, 1992). 'Marion' is the leading trailing blackberry cultivar, accounting for almost 60% of the hectareage planted in Oregon, and is considered to be of the highest quality for processing due to its unique, good flavor (Strik, 1992). 'Kotata' has greater vigor, cold tolerance, fruit firmness, and a good flavor, but 'Marion' blackberries are currently preferred (Strik, 1996).

Trailing blackberries are very vigorous and can be grown in both every-year (EY) and alternate year (AY) production systems. In EY production, fruit is produced every year, and in AY production, fruit is produced every other year. There has been little research on trailing blackberry production and physiology, especially concerning the AY production system.

In AY production, 70 to 90% of the yield of the traditional EY system is produced over a two year period (Bullock, 1963; Nelson and Martin, 1989; Sheets *et al.*, 1975). The overall production cost is lower in the AY system due to less labor needed for pruning and training, reduced disease and cold injury, minimized damage to primocanes during machine harvest, and less fertilizer and pesticide inputs (Sheets *et al.*, 1975, 1987).

Most nitrogen studies with blackberries have been conducted on EY production systems. Nelson and Martin (1986a; 1986b) did two nitrogen fertilization studies on 'Thornless Evergreen' blackberries in the EY system, showing that the rate of applied nitrogen was significantly correlated with the yield. In a fertilization study on 'Hull Thornless' blackberries, Archbold *et al.* (1989) also found

yield to be correlated with applied nitrogen. However, no correlation was found between applied N and yield in 'Arapaho' thornless erect blackberry (Alleyne and Clark, 1997; Naraguma and Clark, 1998).

Split applications of N are more efficient in some crops such as blueberries than single applications (Hanson and Retamales, 1992). No difference in yield was found between single and split N applications to 'Arapaho' thornless erect blackberry (Alleyne and Clark, 1997; Naraguma and Clark, 1998). No research supports split applications in trailing blackberries, and industry practices vary both in timing and rates (Strik, 1998, personal communication). Also, in AY production systems it is not known whether a nitrogen application is necessary in both years or in only one, either the on-year or the off-year. No research has been conducted to determine the importance of the timing of the application and affects of primocane management.

Malik and Archbold (1991) used ^{15}N to study the partitioning of nitrogen over two seasons in pot-grown, semi-erect blackberry, 'Chester Thornless', in the EY system. They found that newly acquired nitrogen was allocated to new growth, such as primocanes, primocane leaves, and fruit, with fruit being the strongest sink. There was a significant loss of total plant nitrogen both from stored reserves and from newly acquired sources as a result of fruit harvest, florican pruning, and leaf senescence. Naraguma *et al.* (1999) used ^{15}N to study 1 and 2 year-old field-grown 'Arapaho' thornless erect blackberry in the EY system. The majority of dry weight was found in the primocanes, primocane leaves, and roots, and newly acquired N was allocated to new growth and fruit. Uptake of fertilizer N by primocanes continued through the fall. No information on nitrogen partitioning patterns in trailing blackberry is yet available.

It is important to apply nitrogen as close as possible to the time of peak demand of the plant. Optimization of N application would not only save growers money and optimize plant growth, but could also reduce the risk of ground water contamination through over-application of N and leaching of N past the root zone.

This research was undertaken to develop a better understanding of the effect of AY production on nitrogen uptake and partitioning in 'Marion' and 'Kotata' trailing blackberries, and to observe how the timing of fertilizer application affects nitrogen uptake and partitioning. The specific objectives of this study were to:

- characterize N-partitioning and remobilization for a two-year period in 'Kotata' blackberry plants grown in AY production,
- determine the influence of time of year of nitrogen fertilizer application on nitrogen partitioning and remobilization in 'Marion' blackberry plants in AY production,
- determine the influence of single, double split, and triple split applications of nitrogen fertilizer on 'Marion' blackberry plants in AY production,
- determine if 'Marion' blackberries in AY production require nitrogen fertilization in both the on- and off-years, or only one.

Review of the Literature

Description of the Trailing Blackberry Industry

Three types of blackberries are grown in the United States, erect, semi-erect, and trailing. Trailing blackberries predominate in the Pacific Northwest, while erect and semi-erect blackberries are mainly grown in the southern and eastern regions of the United States (Himelrick, 1993; Lipe and Martin, 1984). Approximately 95% of the blackberries grown in Oregon are trailing, such as 'Marion', 'Boysen', and 'Kotata' (Strik, 1992). Oregon produces 85% of the blackberries used for commercial processing in the United States, and is the leading blackberry producer in the world (Strik, 1992). According to the Oregon Agricultural Statistics Service (Anonymous, 1998) over 2755 hectares of trailing blackberries are currently grown in Oregon. About 98% of the crop goes to processing for products such as IQF (Individually Quick Frozen), straight or sugared frozen fruit, and purees (Strik, 1996).

'Marion', 'Thornless Evergreen', and 'Boysen' are the most important trailing blackberry cultivars in the Pacific Northwest (Strik, 1992). 'Marion' accounts for almost 60% of the hectareage planted in Oregon (Anonymous, 1998), and is considered to have one of the highest quality for processing due to its unique, good flavor (Strik, 1992).

Due to greater vigor, cold tolerance, and firmness, 'Kotata' was released in 1984 as a possible replacement for 'Marion', and although the flavor is good, 'Marion' blackberries are currently preferred (Strik, 1996). According to Finn *et al.* (1996) the marketing of the 'Marion' name is the primary reason that 'Kotata' is not more widely planted. However, 'Kotata' blackberry hectareage is increasing in Oregon, as fruit are similar in quality to 'Marion' but firmer (Moore and Skirven, 1990; Strik, 1992).

Both 'Kotata' and 'Marion' are quite compensatory for primary bud loss, with 'Kotata' blackberries having no loss of yield even when 75% of the primary buds

were removed (Strik *et al.*, 1996). Bell *et al.* (1992) found 'Kotata' blackberries to be more winter cold hardy than 'Marion'. Both 'Kotata' and 'Marion' are very vigorous plants, but 'Kotata' is significantly more productive (Finn *et al.*, 1996).

Alternate-Year and Every-Year Production Systems

In blackberry, the roots and crowns are perennial, but the shoots are biennial. Blackberry shoots are vegetative the first year (primocanes) and productive the second year (floricanes), after which the floricanes die. Two production systems currently used to grow trailing blackberries are the alternate-year (AY) and every year (EY) systems. In the EY production system, fruit is produced every year, with primocanes and floricanes present on the plant. After harvest, the floricanes are removed and the primocanes trained onto the trellis. In the AY production system, fruit is produced every other year. Only primocanes grow the non-production year (off-year): these become floricanes the following year (on-year). After harvest, all the canes are removed in October, and a new cycle begins. Usually half of the field will be in production each year. There has been little research on trailing blackberry production and physiology, especially concerning AY and EY production systems.

Sheets *et al.* (1975, 1987) compiled a list of advantages and disadvantages of AY production. Advantages included a lower overall production cost due to less labor for pruning and training, reduced disease and cold injury, minimized damage to primocanes during machine harvest, and less fertilizer and pesticide inputs. A cost study comparing AY to EY production over an eleven year period showed that EY production had an average cost of \$.88/kg, while AY was only \$.79/kg (Burt *et al.*, 1987).

In AY production, 70 to 90% of the yield of the traditional EY system is produced over a two year period (Bullock, 1963; Nelson and Martin, 1989; Sheets *et al.*, 1975). During the off-year of the AY system, blackberry plants produce many more primocanes than in EY production when floricanes are present (Cortell and

Strik, 1997a; Sheets and Kangas, 1970; Strik *et al.*, 1996). Nelson and Martin (1989) found 'Boysen' trailing blackberries grown in the AY system produced significantly more canes, higher yields, and smaller fruit than those grown in the EY system.

Winter injury can be a very serious problem with 'Marion' blackberries. At about -13°C, 'Marion' and 'Boysen' are damaged. Damage can occur at even higher temperatures in late winter when a cold spell follows a warm spell (Strik, 1996). At least six times since 1950, winter damage has reduced crop yield by more than 25% (Bell *et al.*, 1995). 'Marion' blackberries grown in the AY production system have been observed in the field to have greater cold hardiness than when grown in the EY system (Bell *et al.*, 1992; Cortell and Strik, 1997a; Sheets, 1987).

Blackberries grown in the AY system show a reduction in a fungal cane disease caused by *Septocyta ruborum* (Lib.) Petr. and *Septoria rubi* Westend, which reduces pesticide costs for the grower (Strik, 1996).

Despite the advantages of AY production, only 20% of the trailing blackberry hectareage grown in Oregon is in the AY system, a decrease from 55% in the past. Cold events and crop loss may have caused the decrease in percentage (Strik, 1996).

When red raspberries (*Rubus* spp.) were grown in the AY system a general decline in plant vigor occurred over several years (Dalman, 1989, Freeman *et al.*, 1989). Raspberry cultivars vary greatly in their response to AY production, with an average yield increase varying from 0% to 63% when compared to EY production (Waister *et al.*, 1977). In Australia, 'Willamette' grown in the AY system produced 75% of the yield of the EY system (Clark, 1984).

Nitrogen and Blackberries

The earth's atmosphere consists of 78% nitrogen, in the form of N₂, a gas which unfortunately can not be used by higher plants until it is converted to an available form by microorganisms or industrial processes. Sources of inorganic

nitrogen in the root zone include: atmospheric deposition, mineralization of soil organic nitrogen, or the addition of fertilizers (Tisdale *et al.*, 1993).

Atmospheric deposition occurs when nitrogen compounds in the air from industrial sites, lightning, and nitrogen volatilization are returned to the earth in rainfall (Tisdale *et al.*, 1993). Mineralization of nitrogen is a microbial process in which proteins, amino sugars, and nucleic acids are degraded to ammonium (NH_4^+), the mineral form of nitrogen (Paul and Clark, 1989). Fertilizer nitrogen additions include inorganic synthetic fertilizers and organic manure and legume-N. Manure is a good source of nutrients, but requires greater management skills than synthetic or chemical fertilizers due to its variable nutrient content, increased handling, and nutrient release characteristics (Hart *et al.*, 1992).

Losses of inorganic nitrogen from the root zone include crop uptake and removal, volatilization, denitrification, and leaching. A commercially grown mature blackberry plant can have a dry mass ranging from 4 to 8 kg (Cortell and Strik, 1997b). If the nitrogen content is between 2% and 3% (Pritts and Handley, 1994), then a blackberry plant could consist of 80 to 240 g N per plant (a rate of 35 –209 $\text{kg}\cdot\text{ha}^{-1}$). Nitrogen losses due to volatilization of N depend on many factors such as soil type and temperature, and are very sensitive to the form of N fertilizer (Tisdale *et al.*, 1993). When soils are low in O_2 , as when they are waterlogged, many microorganisms can obtain their oxygen from NO_2^- and NO_3^- releasing the N as a gas; a process called denitrification.

Nitrate movement into the groundwater by leaching is a major concern (Keeney, 1982; and Strebel *et al.*, 1989), so it is important to apply nitrogen as close as possible to the time of peak demand of the plant. However, Oregon State University recommendations for trailing blackberries suggest nitrogen at 56 to 78 $\text{kg}\cdot\text{ha}^{-1}$ in the spring (Hart *et al.*, 1992), which is long before much of the primocane growth occurs (Cortell and Strik, 1997a). Nitrogen uptake was estimated at 15-20% for pears (Sanchez *et al.*, 1991). Blueberries recovered 32% of applied nitrogen in a study by Hanson and Retamales (1989), and less than 15% was found in the topsoil at the end of the season, with more than 50% of the applied N unaccounted for.

The N concentration in the top 0.3 meter of most cultivated soils in the United States ranges between 0.03% and 0.4% (Tisdale *et al.*, 1993). The inorganic forms of nitrogen found in the soil include ammonium (NH_4^+), nitrite (NO_2^-), and nitrate (NO_3^-); organic nitrogen is found in proteins, amino acids, amino sugars, and other complex nitrogen compounds (Tisdale *et al.*, 1993). Ninety-five percent or more of the N found in surface soils is present as organic nitrogen, but the dynamic nitrogen cycle involves many transformations between organic and inorganic forms in the plant, soil, and atmosphere (Tisdale *et al.*, 1993).

Nitrogen is an essential plant nutrient for the production and composition of amino acids, proteins, enzymes, and nucleic acids (Marschner, 1995), and is usually between 2% and 3% of the blackberry plant dry matter (Hart *et al.*, 1992; Pritts and Handley, 1994). Nitrogen is the most frequently deficient nutrient in crop production, so understanding its behavior is essential for maximizing agricultural productivity and reducing the impacts of nitrogen on the environment (Tisdale *et al.*, 1993).

Plant roots take up inorganic nitrogen mainly in the form of ammonium and nitrate (Marschner, 1995). Most plants do best with N supplied mostly as NO_3^- with a small proportion as NH_4^+ (Marschner, 1995). Blackberry plants more readily use the nitrate form (Hart *et al.*, 1992).

Oregon State University recommendations for trailing blackberries suggest nitrogen at 56 to 78 $\text{kg}\cdot\text{ha}^{-1}$ in the spring (Hart *et al.*, 1992). For the northeastern United States, Pritts and Handley (1994) recommend a range of 34 to 68 kg N ha^{-1} , depending on the type of soil present.

Little nitrogen research on trailing blackberries has been completed. Sheets and Kangas (1970) applied nitrogen to blackberries grown in the AY and in the EY system fertilized in either the on-year and off-year, or only in the on-year. They suggested there may be no advantage to fertilizing blackberries in both years, for yields were not different from when the plants received fertilizer in the on-year only. No research has been conducted to determine the importance of the timing of the application and how it is affected by primocane management.

Nutrient status of primocane leaves is thought to be an indicator of next year's crop, and is used for fertilizer application recommendations (Hughes *et al.*,

1979). Hart *et al.* (1992) suggests that a late July – early August sampling of primocane leaves should be between 2.3% and 3.0% nitrogen.

Nelson and Martin (1986a; 1986b) did two nitrogen fertilization studies on 'Thornless Evergreen' blackberries in the EY system, showing that the rate of applied nitrogen was significantly correlated with the yield, but there was no consistent relationship of leaf nitrogen levels with yield. In a fertilization study on 'Hull Thornless' erect blackberry, Archbold *et al.* (1989) found yield was correlated with applied nitrogen. However, no correlation was found between applied N and yield in 'Arapaho' thornless erect blackberry (Alleyne and Clark, 1997; Naraguma and Clark, 1998).

Cortell and Strik (1997a) showed that in an EY system from 50 to 60% of the primocane growth in 'Marion' occurs after fruit harvest with individual final cane lengths ranging from 6 to 9 m. However, the current fertilization recommendations suggest nitrogen application in the spring, long before most primocane growth occurs (Hart *et al.*, 1992).

Pritts and Handley (1994) state that a split application of nitrogen is more efficient in *Rubus* spp. than a single application, but no research has been conducted on split applications in trailing blackberry in AY production. In EY production, no difference was found in the yield of 'Arapaho' thornless erect blackberry between single or split N applications (Alleyne and Clark, 1997; Naraguma and Clark, 1998). Although no differences were found in yield, Naraguma *et al.* (1999) found higher leaf N in the split than the single N application.

In apples, the main peak of root growth begins after shoot growth decreases (Atkinson and Wilson, 1980). In a study with fruiting and de-fruited apple trees, N in the de-fruited trees (where fruit sink is missing) was allocated to the roots (Hansen, 1980). Perhaps this could be occurring in the off-year blackberry plants in the AY system, as the fruit sink is absent.

The use of stable isotopes is now common in nitrogen research because the isotope can be used as a tracer of the fertilizer-N in the plant system (Hauck and Bremner, 1976). N-15, a stable isotope of nitrogen, has been used to research many horticultural crops, including almonds (Weinbaum *et al.*, 1984), citrus trees

(Feigenbaum *et al.*, 1987), apple trees (Grasmani and Nicholas, 1971), grapes (Hanson and Howell, 1995), pears (Sanchez *et al.*, 1991), blueberries (Retamales and Hanson, 1989), and semi-erect and erect blackberries (Malik *et al.*, 1991; Naraguma *et al.*, 1999) but there has been no research on trailing blackberries using nitrogen isotopes.

Malik *et al.* (1991) used ^{15}N to study the partitioning of nitrogen over two seasons in pot-grown, semi-erect blackberry, 'Chester Thornless', in the EY system. They found that newly acquired nitrogen was allocated to new growth, such as primocanes, primocane leaves, and fruit, with fruit being the strongest sink. Limited nitrogen turnover or remobilization was shown in the floricanes. There was a significant loss of total plant nitrogen both from stored reserves and from newly acquired sources as a result of fruit harvest, floricanes pruning, and leaf senescence.

Studying 1 and 2 year-old field-grown 'Arapaho' thornless erect blackberry in the EY system, Naraguma *et al.* (1999) used ^{15}N to determine allocation, redistribution, and recovery of fertilizer N. The majority of dry weight was found in the primocanes, primocane leaves, and roots. Newly acquired N was allocated to new growth and fruit. Uptake of fertilizer N by primocanes continued through the fall. The study suggested that floricanes N was translocated to other tissues before death. Fertilizer nitrogen recovery for 'Arapaho' was 32% by October, and 13% of the applied N was accounted for in the soil. No information on N partitioning patterns in trailing blackberry is yet available.

Using ^{15}N , Sanchez *et al.* (1992) found that a fall application of nitrogen to 'Comice' pears stayed mainly in the root storage tissue, and little went to the leaves. About 45% of the stored nitrogen in pears was partitioned to new growth, and fruit and new growth were very dependent on fertilizer nitrogen (Sanchez *et al.*, 1991).

Hanson and Retamales (1989) used ^{15}N to study the efficiency of fertilizer use by highbush blueberry plants. They found fertilizer-derived nitrogen in the leaves two weeks after application. The plants recovered 32% of the applied nitrogen, and less than 15% remained in the soil by the end of the growing season. More than half the applied nitrogen could not be accounted for in the plant and upper 15 cm of soil, and was possibly lost due to leaching, denitrification,

ammonium volatilization, or uptake by the surrounding vegetation. Throop and Hanson (1997) studied the effect of application date on absorption of nitrogen by highbush blueberries, and found plants absorbed nitrogen more efficiently during periods of active growth, in May, June, and July, than in April, August, or September. Plant uptake of nitrogen seemed more affected by need than soil nitrogen availability.

CHAPTER 2: NITROGEN PARTITIONING AND REMOBILIZATION IN FIELD-GROWN 'KOTATA' BLACKBERRIES GROWN IN ALTERNATE YEAR PRODUCTION OVER TWO SEASONS.

Abstract

To study the uptake and partitioning of nitrogen, mature 'Kotata' blackberries (*Rubus* L. subspecies *Rubus* Watson) growing in the alternate year system in the field, were treated with ammonium sulfate depleted in ^{15}N in Spring, 1997. Whole plants were destructively sampled throughout the growing season. In the second year, only non-labeled ammonium sulfate was applied so redistribution could be measured. Whole plants were destructively harvested as in 1997. Total dry weight increased linearly in the off-year (non-producing), but not in the on-year. The greatest percentage of total dry weight was in the primocanes in the off-year and in the fruiting laterals in the on-year. On-year plants had greater dry weight than off-year plants. The season following ^{15}N fertilization, concentration of N generally decreased throughout the season, but the percentage of N from the fertilizer (NDFP) increased linearly in all tissues in on- and off-year plants. N content increased at least through July, indicating a split application of fertilizer would be more effective than a single one. In the off-year, fertilizer N was allocated to new growth (primocanes and primocane leaves). In the on-year, new fertilizer N was also allocated to new growth (fruiting laterals and fruit, primocanes and primocane leaves). The year after fertilization with ^{15}N , percent and N content were similar to the previous year, but the % NDFP decreased linearly in all tissues except the crown and floricanes. In the off-year, stored N was found mainly in the crown, with some allocation to new growth. In the on-year, stored N was allocated towards the floricanes, laterals, and again, fruit was a strong sink. Very little stored N was allocated to the primocanes and primocane leaves in on-year plants. The decrease in N content at the end of the season in tissues that would be lost due to leaf

senescence and fruiting cane death such as primocane leaves, floricanes, and laterals, and an increase in the remaining tissues such as primocanes and crowns suggested remobilization of N. From 22 - 25 g N was removed from the plants at fruit harvest. A substantial amount of N (between 11 and 18 g N/plant) was lost from the blackberry plant when the dead floricanes and laterals were removed in October. Excluding the roots, almost 30% of the applied fertilizer was accounted for by the end of the season of 1997 in both the on- and off-year plants.

Introduction

In blackberry plants, roots and crowns are perennial, but the shoots are biennial. Blackberry shoots are vegetative the first year (primocanes) and reproductive the second year (floricanes), after which the floricanes die. Two production systems currently used to grow trailing blackberries are the alternate-year (AY) and every year (EY) systems. In the EY production system, fruit is produced every year, with primocanes and floricanes present on the plant. After harvest, the floricanes are removed and the primocanes trained onto the trellis. In the AY production system, fruit is produced every other year. Only primocanes grow in the non-productive year (off-year); these then over-winter, becoming floricanes the following year (on-year)(Strik, 1992). After harvest, all the canes are removed in October and a new cycle begins. Usually half of the field will be in production each year. There has been little research on trailing blackberry production and physiology, especially concerning AY and EY production systems.

Sheets *et al.* (1975, 1987) compiled a list of advantages and disadvantages of AY production. Advantages included less labor for pruning and training, reduced disease and cold injury, lowered production costs, minimized damage to primocanes during machine harvest, and less fertilizer and pesticide inputs.

A cost study comparing AY to EY production over an eleven year period showed that EY production had an average cost of \$.88/kg, while AY was only \$.79/kg (Burt *et al.*, 1987).

In AY production, 70 to 90% of the yield of the traditional EY system is produced over a two year period (Bullock, 1963; Nelson and Martin, 1989; Sheets *et al.*, 1975). During the off-year of the AY system, blackberry plants produce more primocanes than in EY production, when floricanes are present (Cortell and Strik, 1997a; Sheets and Kangas, 1970; Strik *et al.*, 1996). Nelson and Martin (1989) found 'Boysen' trailing blackberries grown in the AY system produced significantly more canes, higher yields, and smaller fruit than those grown in the EY system.

When red raspberries (*Rubus* spp.) were grown in the AY system a general decline in plant vigor occurred over several years (Dalman, 1989, Freeman *et al.*, 1989). Raspberry cultivars vary greatly in their response to AY production, with an average yield increase varying from 0% to 63% when compared to EY production (Waister *et al.*, 1977).

Nitrogen is the most frequently deficient nutrient in crop production, so understanding its behavior is essential for maximizing agricultural productivity and reducing the impacts of nitrogen on the environment related to the mobility of nitrate in soil (Tisdale *et al.*, 1993). Nitrogen usually accounts for 2% to 3% of blackberry plant dry matter (Hart *et al.*, 1992; Pritts and Handley, 1994).

Oregon State University recommendations for trailing blackberries suggest nitrogen at 56 to 78 kg·ha⁻¹ in the spring (Hart *et al.*, 1992). For blackberries in the northeastern United States, Pritts and Handley (1994) recommend a range of 34 to 68 kg·ha⁻¹.

Little research on nitrogen use in trailing blackberries has been completed for AY production systems, most has been with EY production systems. Sheets and Kangas (1970) applied nitrogen to blackberries grown in the AY system fertilized in either the on-year and off-year, or only in the on-year. They suggested there may be no advantage to fertilizing blackberries in both years, for yields were not different

from when the plants received fertilizer in the on-year only. No research has been conducted to determine the effect of timing of the nitrogen application in an AY production system.

In 'Thornless Evergreen' trailing blackberries in the EY system Nelson and Martin (1986a and b) found that the rate of applied nitrogen was positively correlated with yield, but there was no consistent relationship between leaf nitrogen concentrations and yield. In a fertilization study on 'Hull Thornless' semi-erect blackberries, Archbold *et al.* (1989) found yield was correlated with applied nitrogen. However, no correlation was found between applied N and yield in 'Arapaho' thornless erect blackberry (Alleyne and Clark, 1997; Naraguma and Clark, 1998).

Pritts and Handley (1994) state that a split application of nitrogen is more efficient in *Rubus* spp. than a single application, but no research has been conducted on split applications in trailing blackberry in AY production. In EY production, no difference was found in the yield of 'Arapaho' thornless erect blackberry between single or split N applications (Alleyne and Clark, 1997; Naraguma and Clark, 1998).

Nitrogen-15, a stable isotope of nitrogen, has been used to research uptake and movement of N in many horticultural crops, including almonds (Weinbaum *et al.*, 1984), citrus trees (Feigenbaum *et al.*, 1987), apple trees (Grasmani and Nicholas, 1971), grapes (Hanson and Howell, 1995), pears (Sanchez *et al.*, 1991), blueberries (Retamales and Hanson, 1989), and semi-erect and erect blackberries (Malik *et al.*, 1991; Naraguma *et al.*, 1999). Trailing blackberries have a very different growth habit than erect and semi-erect types, and there has been no research on trailing blackberries using nitrogen isotopes.

The objective of this study was to characterize N uptake, partitioning and remobilization over a two-year period in 'Kotata' blackberry plants grown in an AY production.

Materials and Methods

A ten-year old 'Kotata' blackberry planting on a quatama soil (fine-loamy, mixed mesic Aquatic Haploxeralfs) at the North Willamette Research and Extension Center, Aurora, Ore. was used. Plants were spaced 2.4 m within rows spaced 3.0 m apart. Rows were oriented north to south on level ground. The trellis consisted of posts with two horizontal wires at 1.2 and 1.8 m. Weed management and irrigation followed standard commercial practice. The blackberries were grown in the alternate year system (AY), where the entire plant was cut to just above the crown height in the fall (October) after harvest. Half the field was in production (on-year), while half the field was in vegetative growth (off year), in any given year.

On 5 Apr. 1997, all plants were given a soil application of 500 ml of a 40% (w/v) solution of ammonium sulfate depleted in ^{15}N (0.05 atom % ^{15}N) at a rate of 56 $\text{kg}\cdot\text{ha}^{-1}$ (42 g N/plant). The labeled fertilizer was poured in a 0.5 m diameter circle on and around each crown, followed by 4 liters of water to move the fertilizer into the root zone. Four single plant replicates were randomly selected and destructively harvested on each of five dates throughout the growing season of 1997. Sampling dates for plants growing in the on-year included: 3 weeks after application (24 Apr. 1997), flowering (12 June 1997), fruit maturity (14 July 1997), time of typical florican removal (11 Aug. 1997), and late season (14 Oct. 1997). Plants in the off-year were sampled on the same dates. The experimental design was completely randomized with four single plant replicates in the on- and off-year sections on each sampling date.

On 17 Mar. 1998, of the second year, only non-labeled ammonium sulfate was applied in the same manner and rate as in 1997, so that redistribution of the labeled N applied in 1997 could be measured. Sampling dates for the second year followed the pattern of the first year: 15 Apr. 1998, 18 June 1998, 17 July 1998, and 13 Oct. 1998.

On each sampling date in both years, plants were partitioned into roots, crown, primocanes, primocane leaves, floricanes, fruiting laterals, and immature and

ripe fruit, if present. Due to the difficulty of excavating the entire root system, a subsample was taken from the root tissues within 0.5 m² of the crown. The separated tissues were air-dried at 60°C to a constant dry weight. Canes were cut into lengths approximately 2-3 inches. Tissues were mixed in large paper bags, and random pieces sampled (total of 50-100 g per tissue) and finely ground to pass a 40-mesh (0.6 mm) screen. Woody crown tissue was subsampled by catching the shavings from drilling 5-10 holes with a 14-mm bit. Two gram subsamples of each of the ground tissues were analyzed for N content and ¹⁵N by mass spectrometry at Isotope Services (Los Alamos, NM). On-year plant total fresh fruit yield was collected every 3 to 5 days throughout the harvest season. Ten fruit per harvest were subsampled with fresh and freeze-dried weight measured. The average of the ten fruit was used to calculate the total fruit dry weight. The freeze-dried fruit were ground and analyzed for N and ¹⁵N.

Atom percent values were converted to the proportion of the nitrogen derived from the fertilizer (NDFF), as described by Sanchez *et al.* 1990 (adapted from Hauck and Bremner, 1976):

$$\text{NDFF} = \frac{(^{15}\text{N}_{\text{natural abundance}}) - (\text{atom } \% ^{15}\text{N})_{\text{tissue}}}{(^{15}\text{N}_{\text{natural abundance}}) - (\text{atom } \% ^{15}\text{N})_{\text{fertilizer}}} ;$$

where ¹⁵N natural abundance was considered equal to 0.365 atom percent.

The presence of any residual ¹⁵N remaining in the soil was determined using barley as an indicator plant. On 4 May 1998, 'Baronesse' spring barley was seeded directly in the areas where the last 8 blackberry plants had been sampled and ON 2 bare check plots. The barley was harvested on 17 July 1998, and analyzed for ¹⁵N.

An analysis of variance (ANOVA) was used to compare the means of the four replications of each tissue type (Systat Version 7.0, SPSS Inc, Evanston, IL 1997). Each sampling date was analyzed separately to compare dry weight, concentration of N and ¹⁵N, and N content and ¹⁵N. Changes in tissue N over time were analyzed by regression. A t-test was used to determine a year effect.

Results and Discussion

Dry weight

By the end of the growing season, 'Kotata' blackberry total dry weight (excluding roots) ranged from 3.1 to 5.4 kg per plant (4.3 to 7.5 t/ha). When years were compared using total dry weight at each sampling date, there was a significant ($P < 0.05$) year effect in the on-year in April, and October (see Appendix A-1 for individual tissue year-effect P-values).

Total dry weight, and dry weight of crowns, primocanes, and primocane leaves increased linearly in off-year plants in both 1997 and 1998 (Figure 2-1, see Appendices A2-4 for more information). On-year total dry weight increased linearly over time in 1998 (Figure 2-1B), but not in 1997 (Figure 2-1C). On-year primocanes and primocane leaves were the only tissues to show a linear increase in dry weight over time in 1997, but in 1998, the crowns did also. Dry weight of floricanes and laterals changed little over time. Raspberry grown in the EY system show a similar pattern to on-year blackberry plants, where primocanes and primocane leaves accumulate dry matter throughout the season into the fall, while floricanes and lateral growth is completed early in the season (Kowalenko *et al.*, 1994a and b).

During the off-year, crowns accounted for the majority of the dry weight in the beginning of the season, but primocanes and primocane leaves exceeded crown dry weight by June (Figure 2-1A and D). In the on-year, an average of 60% of the dry weight (excluding roots) was found in the floricanes and fruiting laterals, and 13% in the primocanes and primocane leaves (Figure 2-1B and C). In comparison, the majority of dry weight of semi-erect blackberries grown in the EY system was found in the primocanes, primocane leaves, and roots (Naraguma *et al.*, 1999; Malik *et al.*, 1991).

Figure 2-1. Dry weight partitioning in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
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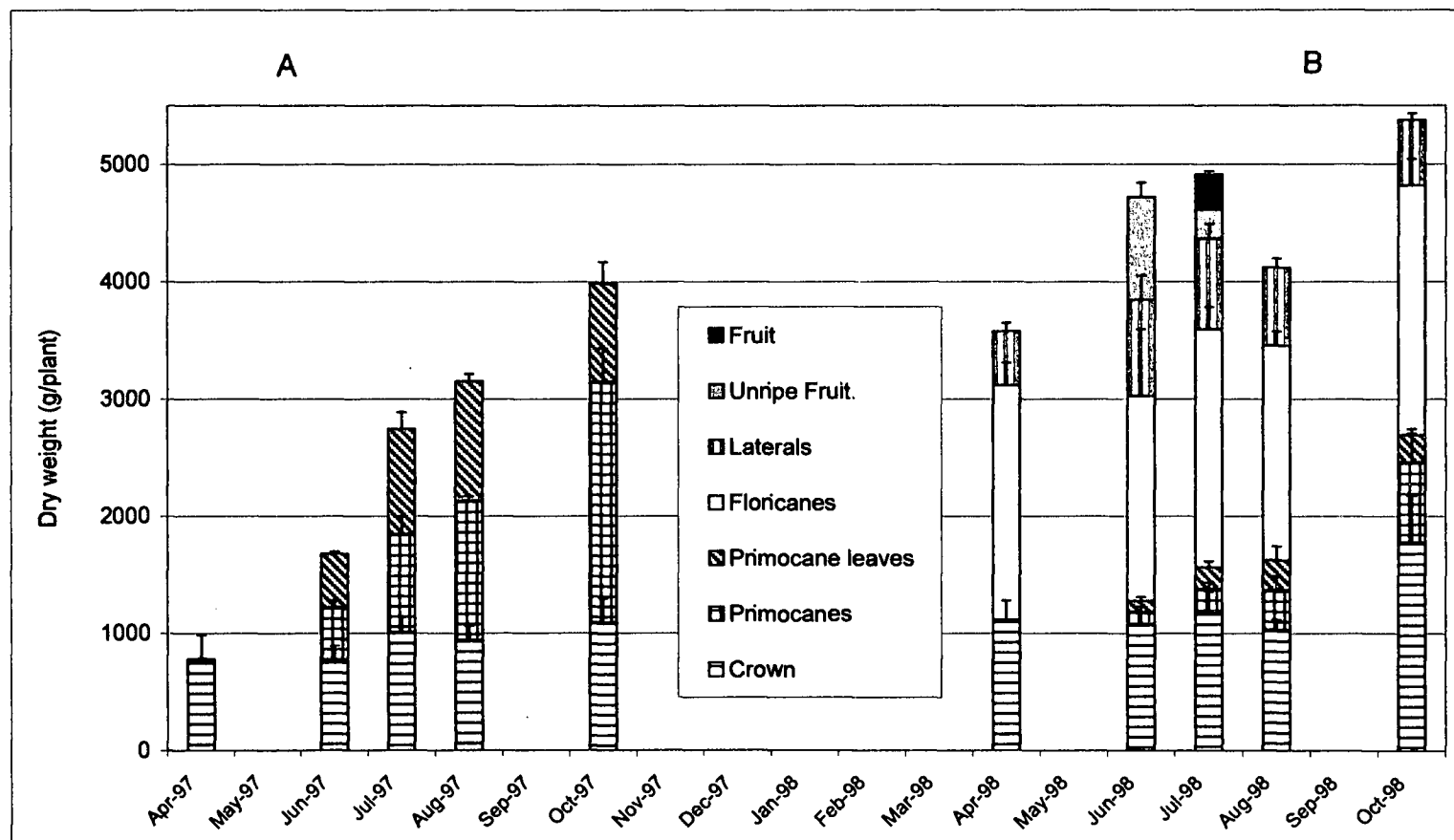
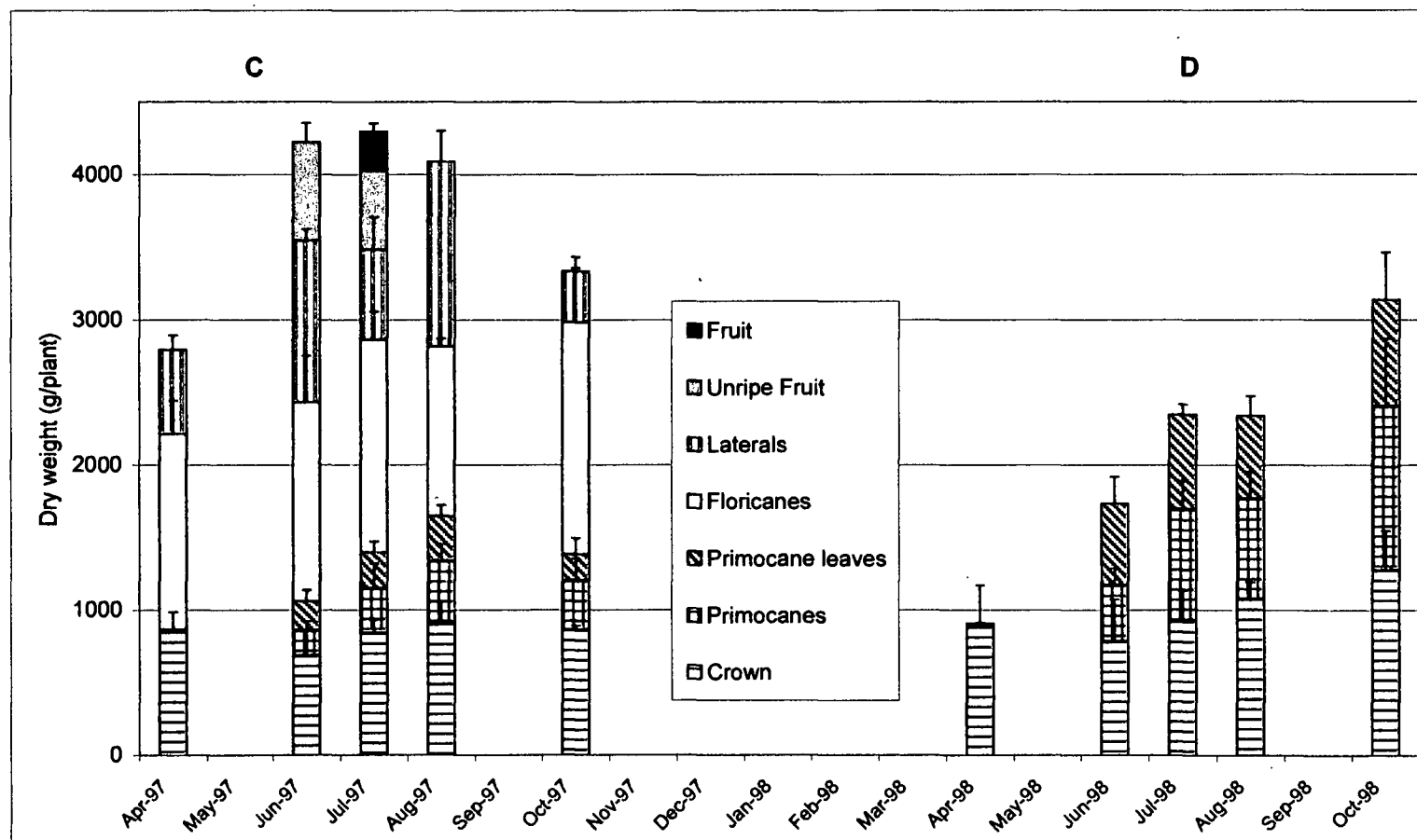


Figure 2-1 (Continued). Dry weight partitioning in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar = 1 SD



On-year total dry weight was significantly greater in both 1997 and 1998 ($P < 0.05$) than the off-year in every month but October of 1997. By the end of the season, off-year primocanes and leaves had over five times more dry weight than on-year primocanes in 1997, and two times the primocane weight of on-year plants in 1998 (Figure 2-1). These findings are similar to other studies involving dry weight partitioning in blackberry (Cortell and Strik, 1997b; Nelson and Martin, 1989; Sheets and Kangas, 1970; Strik *et al.*, 1996). Presumably the lower primocane and primocane leaf dry weight in the on-year is due to the presence of competing sinks including floricanes, fruiting laterals, and fruit.

In on-year plants, an average of 50% of the total primocane growth (dry weight) occurred after harvest. In off-year plants, primocane growth increased an average of 45% during this same period. Cortell and Strik (1997b) found that 45% of the total dry weight content of primocanes in 'Marion' blackberries occurred post-harvest. In red raspberry, about 25% of primocane growth occurred post-harvest (Waister and Wright, 1989).

Fruit were harvested the first three weeks in July every 4 to 6 days (Table 2-1). The second harvest was the largest. Fresh weight yield in 1997 (9.4 kg/plant) was not significantly different than the yield in 1998 (10.0 kg/plant). Mean fruit size was 3.5 g, with an average dry weight content of 17%.

In the on-year, mean crown dry weight tended to decrease from April to June, then increase to surpass the initial weight by the end of the season. This suggests resources in the crown were being used for initial plant growth, and were then replenished and crown growth occurred. A similar pattern occurred in red raspberry, where root dry weight increased with the onset of fruiting, decreased greatly during peak harvest, and was replenished by the end of the growing season (Fernandez and Pritts, 1993). In this study, root dry weight could not be obtained. In a study by Malik *et al.* (1991) potted 'Chester Thornless' blackberries in the EY system had 41% of the total plant dry weight in the roots. Naraguma *et al.* (1999) found roots of 'Arapaho' thornless erect blackberry grown in the EY system contained 26% of the total dry weight (not including fruit). In a study with fruiting

and de-fruited apple trees, N in the de-fruited trees was allocated to the roots (Hansen, 1980). This may also occur in off-year blackberry plants when grown in the AY system, because the fruit sink is absent. In blackberry, it is possible that more root growth occurs in the off-year, where there is no fruit sink, than in the on-year. If so, on- and off-year total plant dry weight differences would not be as great as is seen in this study.

Nitrogen Concentration

There was a year effect on concentration of N in all tissues, except on-year roots and fruiting laterals, on at least one sampling date. Floricanes and crowns contained the lowest concentration of nitrogen in the tissues, averaging 0.7% (Figure 2-2). Unripe fruit, primocane leaves, and laterals contained the highest concentration of N. The concentration of N decreased linearly in all tissues throughout the season except for the crowns, which generally showed little change through the season (Figure 2-2, see Appendices A5 & A6 for more information). There was no significant difference in the N concentration of tissues among the on- and off-years (Figure 2-2).

Hart *et al.* (1992) suggested that a late July – early August sampling of primocane leaves should have an N concentration between 2.3 and 3.0%: 'Kotata' primocane leaves averaged 2.2% in July/August of 1997, and 2.1% in 1998, somewhat below the desired range. It is possible that the rate of N applied ($56 \text{ kg} \cdot \text{ha}^{-1}$) was not sufficient for the vigorous 'Kotata'.

Fruit mean N concentration was 1.4%, with a significant increase during peak harvest to 1.5 and 1.6% (1997 and 1998 respectively) (Table 2-1). Unripe fruit contained almost twice the N concentration as ripe fruit (Figure 2-2).

Figure 2-2. N concentration in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
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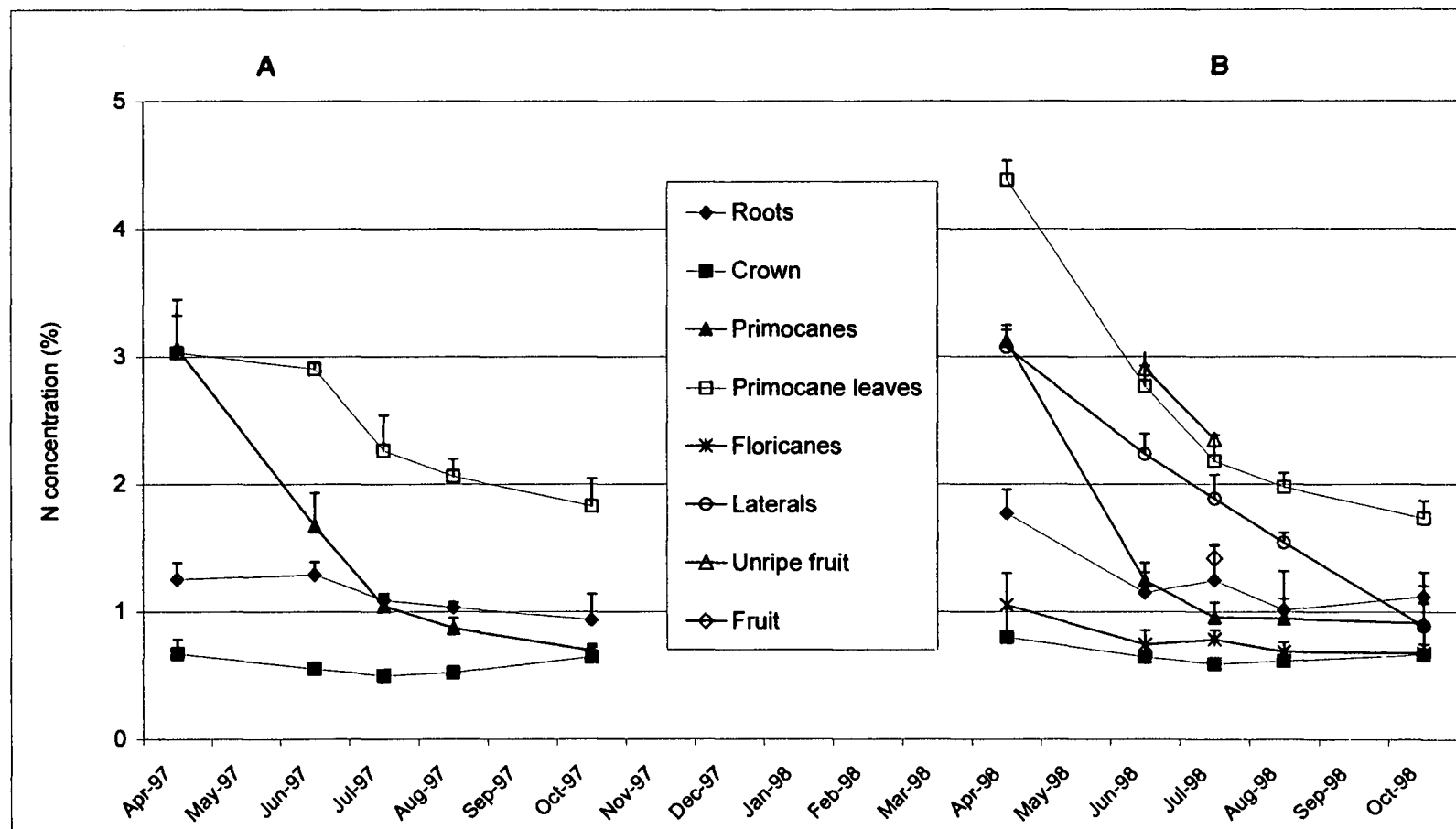


Figure 2-2 (Continued). N concentration in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar \approx 1 SD

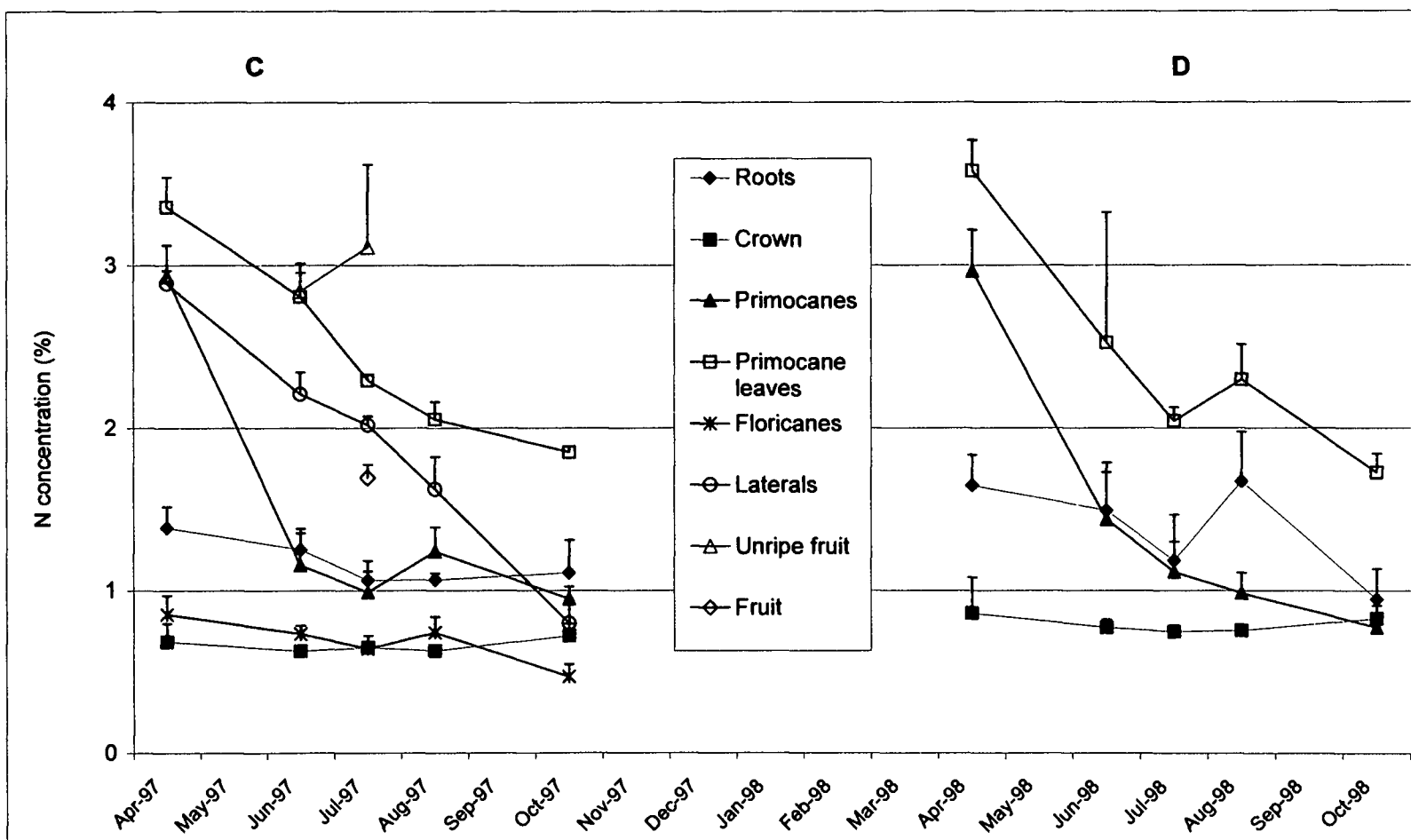


Table 2-1. 'Kotata' yield, fruit weight and nitrogen content, 1997 and 1998.

Harvest date		Total Fresh Yield (kg)	Mean Fruit Weight (g)	Fruit N (%)	Fruit N (g)	Fruit NDFF (%)	Fruit NDFF (g)
1997	7/1	1.83 a	4.4 a	1.4 a	4.6 a	29.8 a	1.4 a
	7/7	2.75 b	4.0 ab	1.5 b	7.7 a	31.7 a	2.5 a
	7/11	1.46 a	4.4 a	1.4 a	3.8 a	32.1 a	1.2 a
	7/16	1.81 a	4.3 a	1.4 a	4.6 a	29.3 a	1.3 a
	7/22	1.57 a	3.6 b	1.4 a	4.1 a	29.6 a	1.2 a
1998	7/2	1.35 a	3.2 a	1.5 ad	3.1 a	21.5 a	0.7 a
	7/7	2.34 b	3.3 a	1.6 ac	5.7 ab	19.6 a	1.1 b
	7/10	1.22 a	3.0 a	1.5 cd	2.8 bc	20.0 a	0.6 ca
	7/14	1.50 ac	3.1 a	1.3 b	2.9 c	20.0 a	0.6 cb
	7/17	1.77 c	3.2 a	1.4 d	3.9 bc	19.1 a	0.7 ca
	7/22	1.77 c	2.0 b	1.5 acd	4.0 d	21.4 a	0.8 cb
'97 vs '98 ^z		0.080	0.000	0.704	0.000	0.000	0.000

^zP-values for year effect - 1997 vs. 1998.

Nitrogen Content

Figures for N content exclude roots, from which a total dry weight could not be obtained. There was a year effect for N content in the plant in August of the off-year, and April, August, and October of the on-year.

During the off-year, total plant N content, and individual tissue N content increased linearly over time (Figure 2-3, see Appendices A7 & A8 for more information). On-year plants had maximum N content in June. In 1997, N content in on-year plants decreased linearly in the floricanes and laterals, increased in the primocanes, while there was no linear relationship in the primocane leaves. In 1998, N content in the on-year plants decreased through the season in the primocanes, primocane leaves, and fruiting laterals, and increased in the crowns.

Figure 2-3. N partitioning in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar = 1 SD

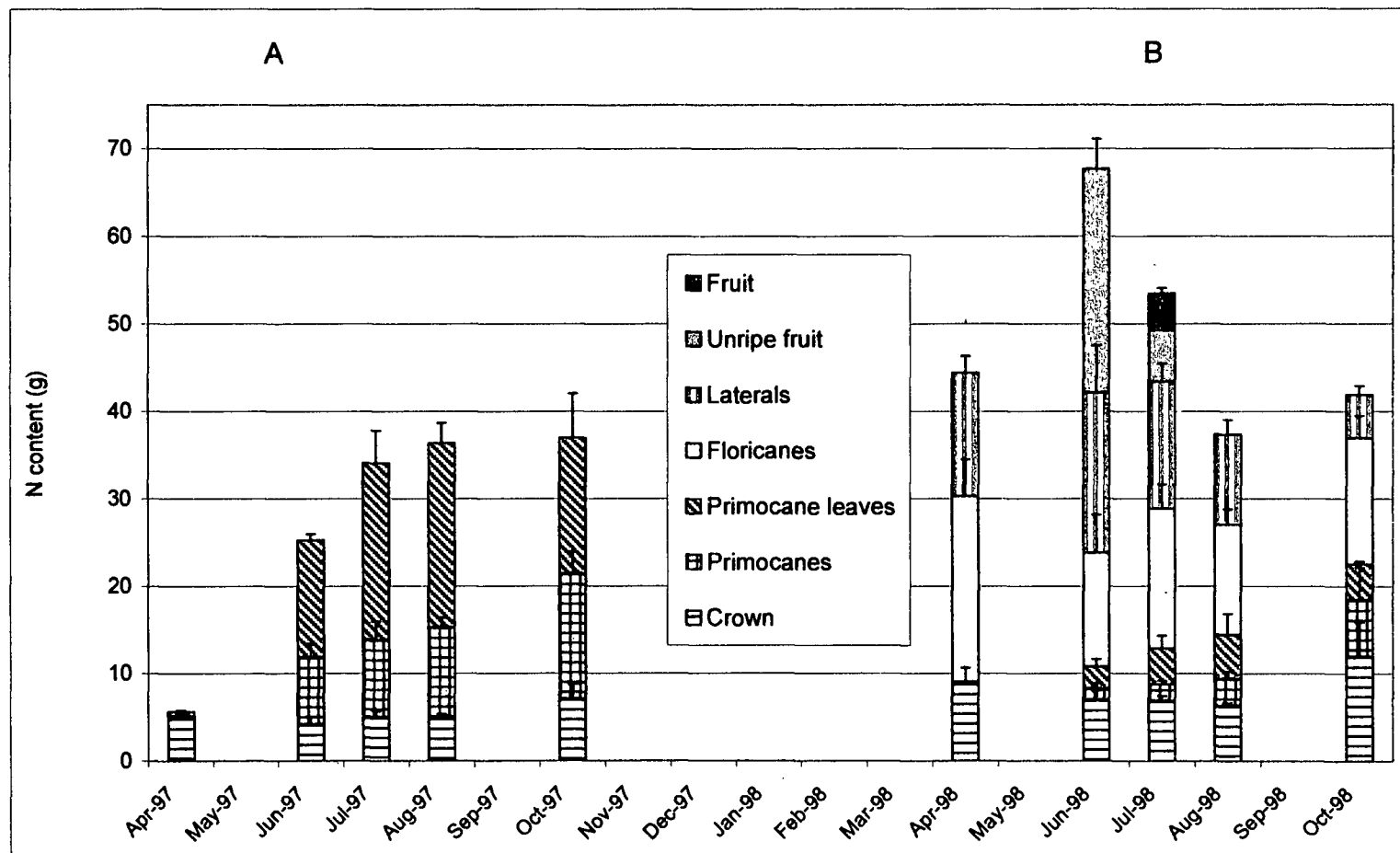
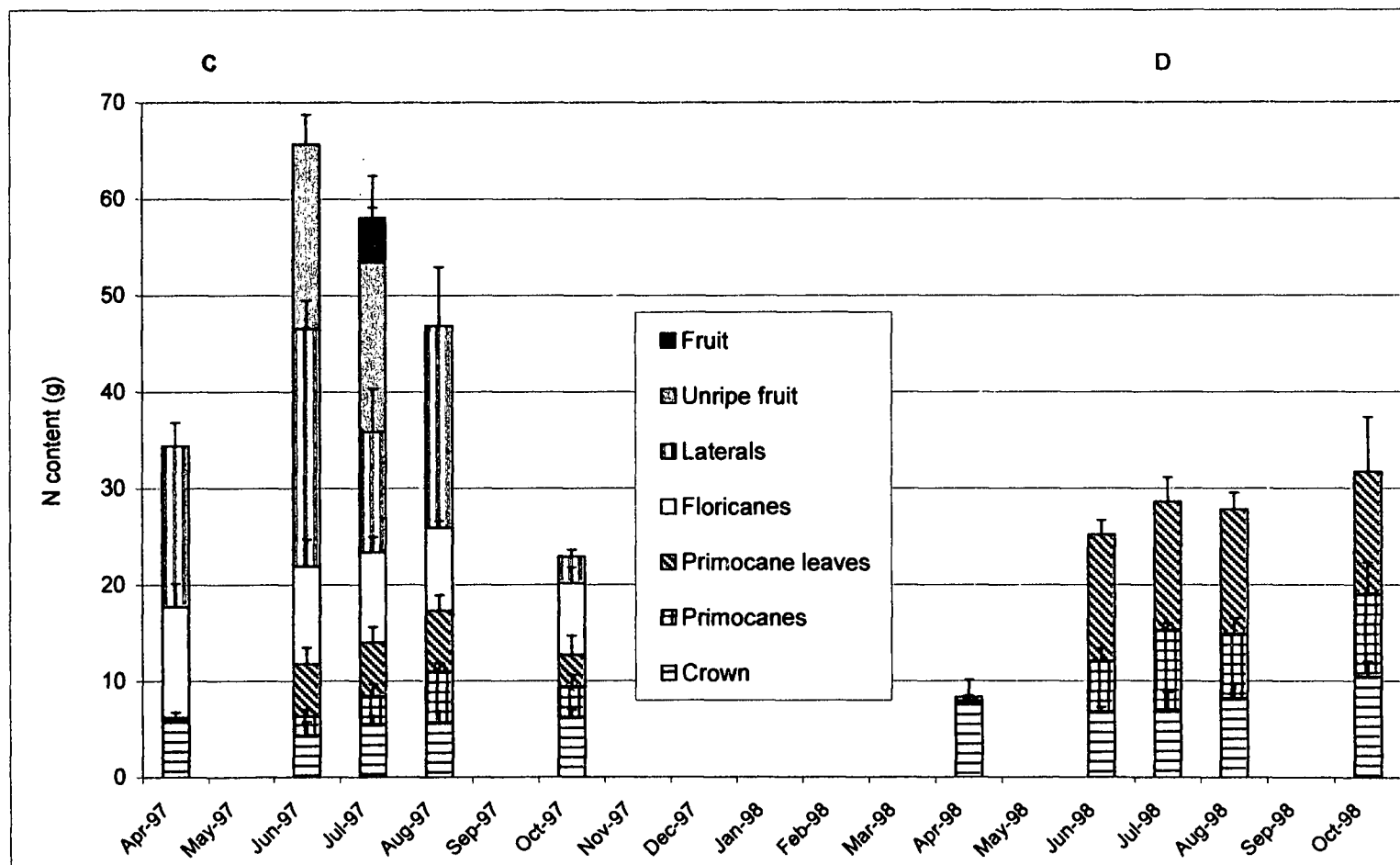


Figure 2-3 (Continued). N partitioning in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar = 1 SD



In 1997, with the exception of April when growth had just started, off-year primocanes and primocane leaves consistently contained a significantly greater quantity of N than the crown. In 1998, off-year primocane leaves had a higher mean N content from April through August than the crown, and a higher mean N content than the primocanes in most months. In 1998, in the on-year, though, the crown contained more N than the primocanes and primocane leaves, except for August, where the crown and primocane leaves were similar. Floricanes and laterals contained a high amount of N in all months but October, where lateral-N decreased significantly (Figure 2-3). The decrease of lateral N could be due to leaf senescence or remobilization of the leaf N, but few leaves had senesced from the plant by the October sampling date. Crown N content increased from August to October in both the on- and off-years.

At the June sampling date, in 1997, unripe fruit contained significantly more N than any other tissue except the laterals, and in 1998 contained significantly more N than any other tissue. In 1997, fruit N content averaged 3.4 g per plant except during peak harvest, where it was 7.7 g. Fruit N content in 1998 followed a similar trend (Table 2-1). Total fruit harvest included 24.8 g N in 1997, and 22.4 g N in 1998.

On-year plant N content was 2 to 3.5 times higher than off-year N in all months but October of 1998, with a high during the fruiting season of about 67 g N per plant, decreasing to a low of 22 g by October (Figure 2-3). Although the on-year fruiting plants took up a greater amount of N, off-year plants still took up a substantial amount; a mean of 37.0 g N/plant in 1997, and 31.8 g in 1998. Sheets and Kangas (1970) suggested no need to fertilize in the on- and off years. This study shows that 'Kotata' take up high amounts of N in both the on- and off-years.

Floricanes and their fruiting laterals die after harvest and leaves are senesced from the primocanes in fall. A decrease in the N content in these tissues between July and October, and an increase in remaining tissues is consistent with remobilization of N before it is lost from the plant. As expected, in the off-year of 1997, primocane leaf N content tended to decrease while crown and primocane N content increased between July and October. In 1998, however, primocane

and crown N content increased, but primocane leaf N content showed no change (Figure 2-3). Since leaves had not yet senesced, remobilization of N from primocane leaves could have occurred later than the mid-October sampling date. In the on-year of 1997, fruiting lateral N content decreased from a mean of 21.0 g in August to 2.8 g in October (Figure 2-3C). Primocane, primocane leaf, and floricanes N content decreased, while the crown had a slight increase in N content from August to October. In 1998 on-year plants had an increase in crown and primocane N content, and a decrease in floricanes, lateral, and primocane leaf N content in the same period. In the AY system, on-year plants are cut to the ground in October, so primocane and leaf N would be lost along with floricanes and laterals. This amounted to 16.7 g N in 1997, and 29.8 g in 1998, lost from the plant. The results show that in an EY production system, growers could reduce crop N loss by removing dead floricanes in October (2.8 g lost) instead of the customary August (21.0 g lost) date. Presumably, this N would go to the crown and/or roots to support early season primocane growth, and may be important for yield potential.

Crop Nitrogen Derived from the Fertilizer (%)

Following fertilization with ^{15}N (1997), all tissues increased linearly over time in the concentration of nitrogen derived from the fertilizer (%NDFF)(Figure 2-4A and C), in contrast to N concentration, which decreased linearly (Figure 2-3A and C)(see Appendices A9 and A10 for more information). In the off-year, crowns had the lowest %NDFF with a maximum of 13% in October. The %NDFF of roots increased from 6.7% in April to 25% in October (Figure 2-4A). The %NDFF of primocanes and primocane leaves increased from about 25% NDFF in April 1997, ending the season at 33% for the primocanes and 37% for the primocane leaves. During the on-year (Figure 2-4C), the highest %NDFF was in the primocanes and primocane leaves averaging 40% June through October. Crown and floricanes %NDFF remained relatively low (13% and 10%, respectively), while root %NDFF rose to

36%. Primocanes and primocane leaves contained the highest %NDFF in both the on- and off-years, with crowns and floricanes having the lowest. Thus fertilizer nitrogen, as opposed to stored N, is predominately used for primocane growth, as in the case for 'Chester Thornless' blackberry (Malik *et al.*, 1991).

An analysis of the 'Baronesse' spring barley seeded in the areas where blackberry plants had been sampled and bare check plots showed a mean of < 0.01% of the N in the barley from the check plots was from ^{15}N , and a mean of 0.01% of the N in the plots where blackberries had been sampled was ^{15}N from the labeled fertilizer. For the purpose of this study, this was a low enough percentage to assume no residual ^{15}N remained in the soil as inorganic N.

Since no ^{15}N had been applied in 1998, it was assumed that the ^{15}N measured in 1997 was from that applied in April of 1997, now stored N. In the off-year, all tissues decreased linearly in % NDFF throughout the season except the crown, which changed little over time (Figure 2-4D). The roots contained the highest %NDFF, from 28% in April to 15% in October, and the primocanes and leaves decreased from 25% NDFF to average 10% NDFF in the same time period (Figure 2-4D). In the on-year, all tissues decreased linearly in % NDFF except for the crowns and the floricanes, which did not show much of a change (Figure 2-4B). The floricanes, roots, and laterals contained the highest % NDFF, with the crown, primocanes, and primocane leaves having the lowest. Similar to red raspberry (Fernandez and Pritts, 1993), during fruit growth (June), root % stored NDFF decreased, and during peak fruit ripening (July), crown % stored NDFF decreased, suggesting movement of stored N from the roots and crowns to the fruit may have occurred.

Mean concentration of NDFF in the fruit in 1998 was 20.2%, significantly different from 1997 (30.5%). Concentration of N in the fruit was not significantly different between 1997 and 1998. Thus, the change in concentration of NDFF shows that fruit are strong sinks for N, and preferentially new fertilizer N. This dependency of fruit for new N is found in many fruiting plants, such as grapes (Hanson and Howell, 1995), pears (Sanchez *et al.*, 1991), and apples (Atkinson *et al.*, 1980; Grasmanis and Nicholas, 1971).

Figure 2-4. NDFF concentration in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
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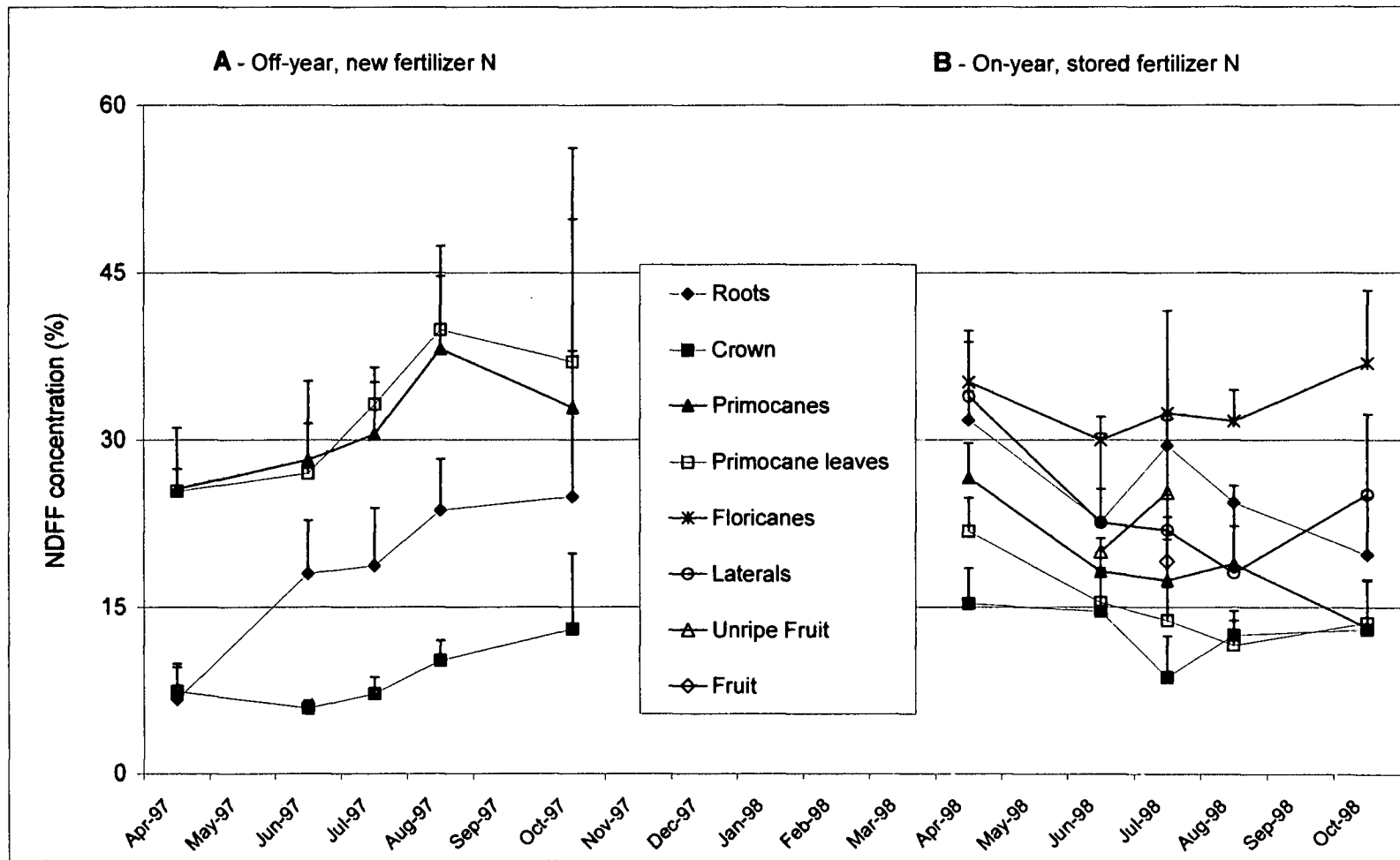
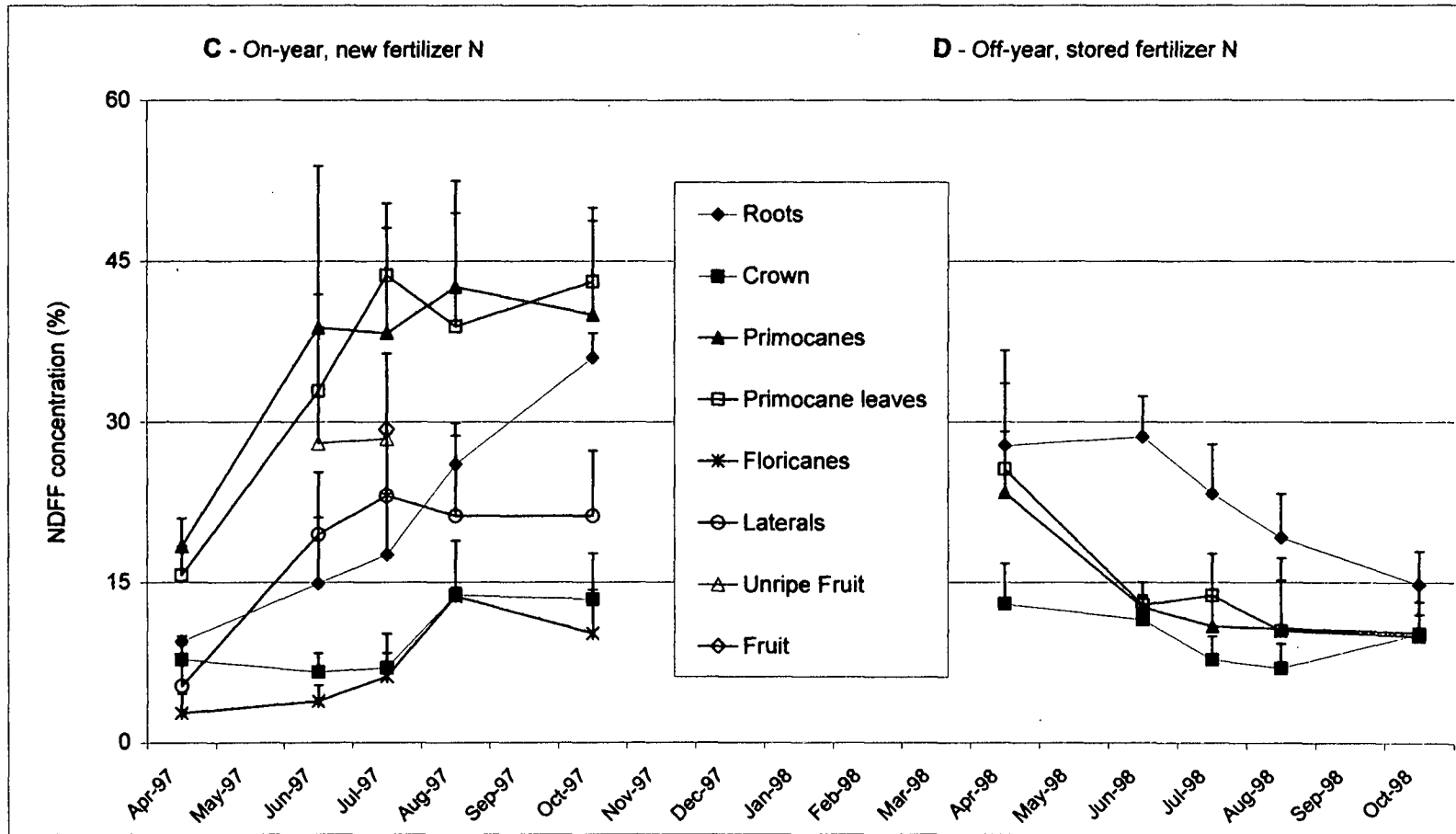


Figure 2-4 (Continued). NDFF concentration in Kotata blackberry. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar = 1 SD



Accumulation of Nitrogen Derived from the Fertilizer – Off-year Application

The content of nitrogen derived from the fertilizer (NDFF) in the blackberry was calculated by multiplying the tissue NDFF concentration by the tissue dry weight. When ^{15}N was applied in the off-year, 1997 (Figure 2-5A see Appendices A11 & A12 for more information), the NDFF content increased linearly over time in all tissues (crowns, primocanes, and primocane leaves) to average 12.4 g NDFF content per plant by October (figures exclude roots) as compared to 36 g N content (Figure 2-3A). At the end of the growing season, between August and October, NDFF content increased in the crown and primocanes, and tended to decrease in the primocane leaves, possibly due to N remobilization before the leaves senesced. Primocane leaves contained the highest NDFF content throughout the off-year season, with a maximum of 8.4 g NDFF content in August. Primocanes reached a high of 6.3 g NDFF content in October, and crowns had a high of 1.0 g (Figure 2-5A).

When N was applied in the off-year, 12.4 g, or 29.5%, of the applied N was accounted for by October of 1997, excluding roots. This amounts to $16.5 \text{ kg} \cdot \text{ha}^{-1}$ of N taken up by the blackberries. Although this figure excludes root N, the value is much below the recommended 56 to $78 \text{ kg} \cdot \text{ha}^{-1}$ (Hart *et al.*, 1992). It is possible that off-year plants have more root growth and N uptake than on-year plants roots, which grow in competition with fruit. Hanson and Retamales (1989) used ^{15}N to study the efficiency of fertilizer use by highbush blueberry plants. The plants recovered 32% of the applied nitrogen, and less than 15% remained in the soil by the end of the growing season. More than half the applied nitrogen in their study could not be accounted for in the plant and upper 15 cm of soil, and was possibly lost due to leaching, denitrification, ammonium volatilization, or uptake by the surrounding vegetation. Nitrogen uptake was estimated at 15-20% for pears (Sanchez *et al.*, 1991). In this study, the 29.5% N recovery is conservative, because it does not account for N in the roots.

At least 6.1 g of the NDFF that remained in the crowns and primocanes, plus 24.5% of the N located in the roots, was fertilizer N available for reserves for the next year's plants (on-year). Since no ^{15}N remained in the soil as inorganic N, all the ^{15}N that was found in the plant in 1998 had to have been from reserves in the primocanes, crown, or roots. Thus, a minimum of 6.3 g of reserve NDFF had to have been in the roots of 1997 to account for the 12.4 g NDFF that were in the plant in October of 1998.

In 1998, these blackberry plants were in the on-year (Figure 2-5B). The NDFF in the tissues represented N applied the year before, or stored in the plant from the year before. Plants averaged 13.6 g NDFF in April (excluding roots). By the end of the second season, NDFF had decreased to 7.8 g, 18.6% of the ^{15}N that was applied in 1997, or 62.9% of N that was actually acquired by the plant in 1997. After two seasons, 'Chester Thornless' blackberries grown in the AY system retained 27% of the total fertilizer N initially required (Malik *et al.*, 1991), which is much less than the 62.9% found in this study. Fruiting lateral total stored NDFF decreased linearly linearly, and the primocane and primocane leaf NDFF increased linearly over time. Crown stored NDFF started higher (1.4 g) than the previous October (1.0 g), possibly due to remobilization of N from roots, leaves, floricanes, and/or laterals after the October sampling date. Crown stored NDFF followed the pattern of % stored NDFF, decreasing to half by July (possible movement of N to fruit), then increasing again by October to 1.1 g. In 1997, off-year primocanes averaged 24.6% (5 g) NDFF, yet when they became floricanes in 1998 they and the laterals that grew from them averaged 35% (12.0 g) stored NDFF, supporting N remobilization possibly from roots, leaves, floricanes, and/or laterals after the October sampling date. Floricanes had consistently more total stored NDFF throughout the season than any other tissue, with a high in April of 7.3 g and a low of 4.0 g during harvest. Laterals had a high of 4.8 g NDFF in April, decreasing to 1.2 g by October (Figure 2-5B). In June, unripe fruit contained 35.0% of the NDFF found in the blackberry plant, and during harvest, fruit (unripe and ripe) contained 18.3%. In a study by Sanchez *et al.* (1991) about 45% of the stored nitrogen in pears was partitioned to new growth and fruit.

Figure 2-5. NDF partitioning in Kotata blackberries. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar = 1 SD

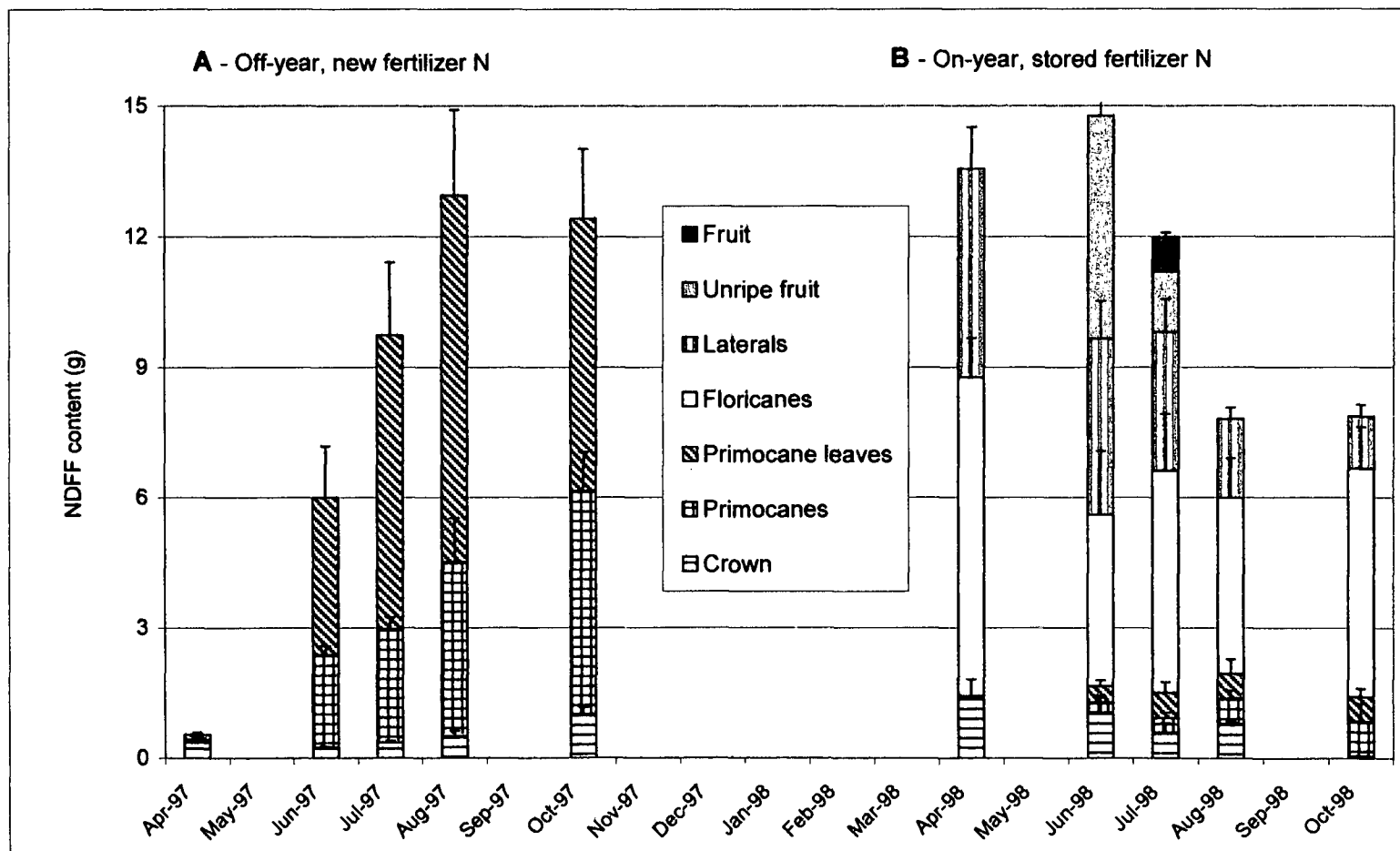
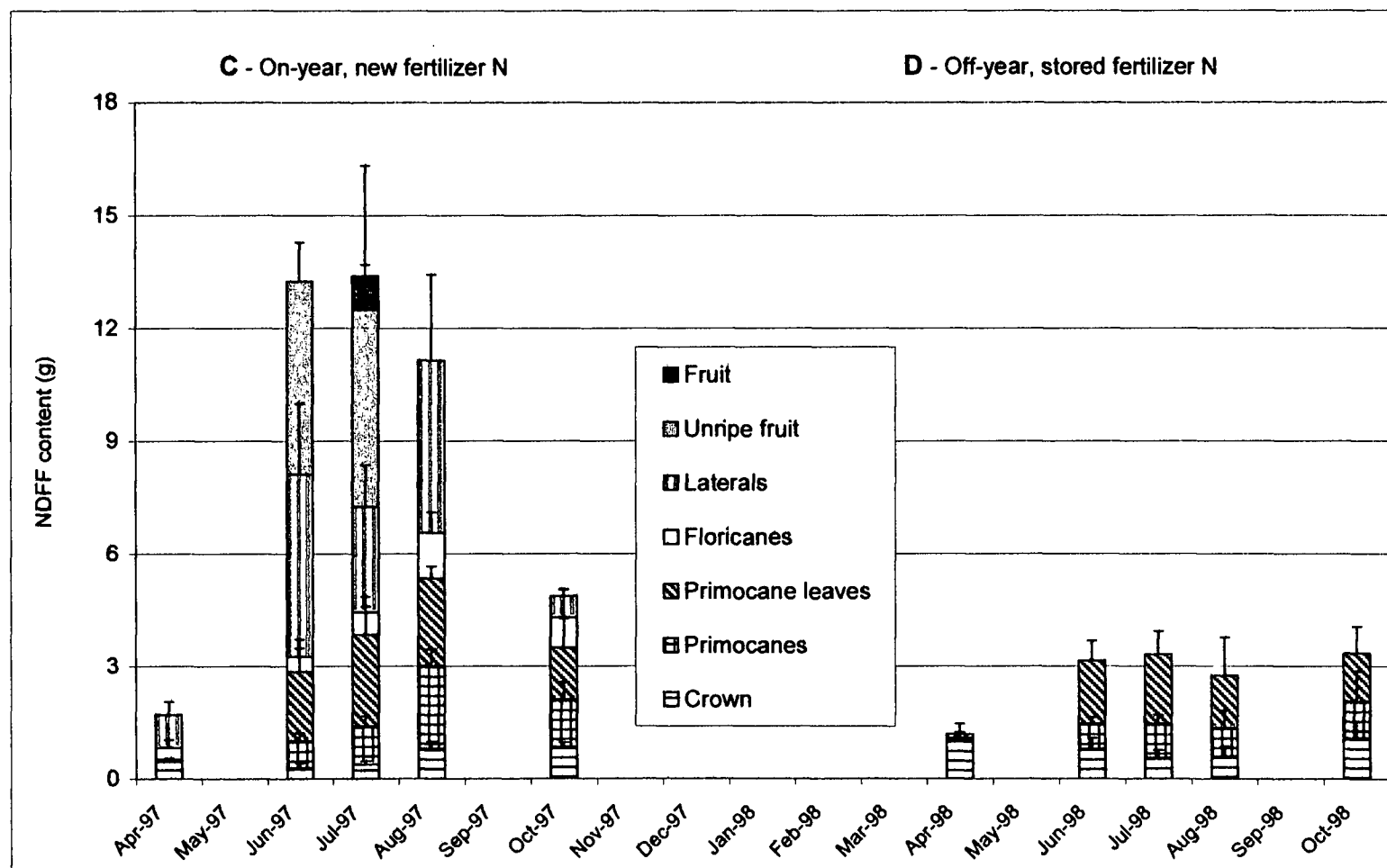


Figure 2-5 (Continued). NDF partitioning in Kotata blackberries. A= off-year 1997, B= on-year 1998, C= on-year 1997, D= off-year 1998
Error bar = 1 SD



Accumulation of Nitrogen Derived from the Fertilizer – On-year Application

When ^{15}N was applied in the on-year, 1997, NDFF content increased greatly from April (1.7 g) to June (13.2 g), and then decreased rapidly from August (11.2 g) to October (4.9 g) (Figure 2-4C). NDFF increased linearly in the crowns and primocanes but decreased linearly in the fruiting laterals (Appendix A-11). In June, unripe fruit contained 39% of the NDFF found in the blackberry plant (excluding roots), and during harvest, the fruit (unripe and ripe) contained 46% of the NDFF. In June and July, unripe fruit contained significantly more NDFF than any other tissue. NDFF in the fruit averaged 1.5 g per harvest and tended to increase during peak harvest to 2.5 g per harvest, totaling 7.6 g NDFF for the fruiting season. In comparison, stored NDFF in the fruit in 1998 decreased significantly to average 0.75 g, with a high of 1.1 g at harvest, totaling 4.5 g (Table 2-1).

Floricanes and laterals die after harvest, and primocane leaves are senesced from the primocanes in the fall. A decrease in the NDFF in these tissues between August and October, and an increase in remaining tissues would support remobilization of N before it is lost from the plant. Leaf senescence occurred after the mid-October sample date, so more remobilization could have taken place after that date. Lateral NDFF greatly decreased from 4.6 to 0.6 g from August to October. NDFF decreased in primocanes, primocane leaves, and floricanes decreased whereas crowns showed no change. For AY production, blackberries are cut to the ground in October, so the 4.0 g NDFF in the primocanes, primocane leaves, floricanes, and fruiting laterals was lost from the plant, and only the 0.8 g N in the crown and what amount was in the roots remained.

In the on-year of 1997, an average of 7.6 g NDFF was lost from the plant in fruit (Table 2-1). By August, the on-year plants had taken up 11.6 g N per plant in the vegetative tissues, totaling 18.8 g N when combined with fruit N. This value amounts to 44.8% of the applied N, or $25.1 \text{ kg} \cdot \text{ha}^{-1}$, accounted for not including the roots (36% of the N in the roots was NDFF).

The following year, the off-year, much less stored NDFF was found in the plant, with the highest total average of 3.3 g in July (Figure 2-4D). However, only 0.8 g NDFF was accounted for in the 1997 crowns that produced this growth, suggesting a large N resource in the roots capable of being remobilized to new growth in blackberry. Total plant and primocane NDFF increased linearly over time. Primocane leaves contained the most NDFF, with a high in July of 1.9 g.

Storage of NDFF from an on-year to an off-year can only be in the crown and roots, since the rest of the plant tissue is removed. The following year, the plants were in the off-year, and by October had a total of 3.4 g NDFF in the crowns, primocanes, and primocane leaves, which was 8% of the ^{15}N applied in 1997. By the end of the second season, NDFF had decreased to 12.9% of the N that was actually acquired by the plant in 1997. After two seasons, 'Chester Thornless' blackberries grown in the AY system retained 27% of the total fertilizer N initially required (Malik *et al.*, 1991), which is double the amount found in this study. Root NDFF started at 27.8% in April, decreasing to 14.8% by October. Assuming that all ^{15}N that could be taken up had been taken up in 1997 in the on-year, the decrease in root and crown % NDFF could have accounted for the increase in the primocane and primocane leaf NDFF.

A nitrogen partitioning study by Malik *et al.* (1991) with pot-grown 'Chester Thornless' erect blackberries grown in the EY system contrasted in many ways with this study. In their study, at the end of the growing season, the majority of the dry weight was found in the roots and primocanes, as compared to the majority of dry weight in the on-year 'Kotata' plants being in the floricanes. At the end of the growing season, floricanes accounted for an average of only 6.6% of the total dry weight of the 'Chester Thornless' blackberry plants (Malik *et al.*, 1991). In this study, floricanes averaged 43.8% of the dry weight. Leaves (floricane and primocane) contained the majority of N in 'Chester Thornless' and floricanes contained the least (Malik *et al.*, 1991). In contrast, 'Kotata' on-year primocane leaves did not account for very much of the total plant N, while the floricanes and laterals (which included leaves) did. Stored N in 'Chester Thornless' went to the floricanes, fruit, and roots

(Malik *et al.*, 1991), similar to what we found in 'Kotata'. Whether the differences in the dry weight and nitrogen partitioning in these studies are due to blackberry type (erect vs. trailing), plant age (young vs. mature), growing conditions (pot vs. field), production system (EY vs. AY), or a combination of these factors is unknown.

In 1997, on-year plant NDFF was greater than off-year NDFF in March through July, but was lower from August through October (Figure 2-4C). Apparently, more N is stored and remobilized for the next year between an off- and on-year, than between an on- and off-year. Contrary to Sheets and Kangas (1970), who suggested fertilizing in the on-year only, this shows the need of new fertilizer N for new growth such as the primocanes and primocane leaves in an off-year. Fertilizing in only the on-year would limit new growth potential in the off-year.

Pritts and Handley (1994) state that a split application of N is more efficient than a single application, but no research has been conducted on split applications in blackberry. Oregon State University recommendations for trailing blackberry suggest nitrogen at 56 to 78.4 kg·ha⁻¹ in the spring (Hart *et al.*, 1992). Fertilizer N was taken up by the blackberry plant at least through July of each year, in both the on- and off-year plants, indicating a split application of N could be more efficient than a single one in the spring.

Summary

When 'Kotata' blackberries were grown in the alternate year system, gain in total dry weight was linear in the off-year, the period of vegetative growth. During the on-year, dry weight increased over time until fruit harvest. During harvest there was a large loss of dry weight as fruit, and after harvest dry matter increased or decreased (1998 and 1997 respectively).

The majority of growth in the off-year occurred in the primocanes, whereas in the on-year most was in the fruiting laterals. On-year plants had a significantly greater total dry weight than off-year plants.

The N concentration generally decreased throughout the season in both on- and off-year plants. However, accumulation of N increased rapidly until about July in both on- and off-year plants. The season following ^{15}N fertilization, the percentage of N derived from the fertilizer (NDFF) increased linearly in all tissues except floricanes. The year after fertilization with ^{15}N , % NDFF decreased linearly in all tissues except for the crowns and floricanes.

The decrease in N content at the end of the season in tissues that were lost due to leaf senescence and fruiting cane death, and an increase in the remaining tissues suggested remobilization of N, especially from the fruiting laterals. Data on N content from the roots could have helped determine the extent of remobilization of N to and from storage tissues.

A substantial amount of N (between 11 and 18 g N/plant) was lost from the blackberry plant when the dead floricanes and laterals were removed in October. Another large loss (22 – 25 g N) was from harvesting the fruit.

In the on-year, stored N was allocated to the floricanes, laterals, and again, fruit was a strong sink. Very little stored N was allocated to the primocanes and primocane leaves of the on-year plants. This study showed the need for fertilizer N in both the on-year, for fruiting lateral and fruit growth, and in the off-year, for new primocane and primocane leaf growth.

Excluding roots, by the end of the 1997 season, almost 30% of the applied fertilizer was accounted for in the off year plants, and 63% accounted for in the on-year plants. Due to the extensive root system, and high root %NDFF found in blackberry, recovery of fertilizer N was likely considerably greater than given values. Between 16.5 and 35.2 kg·ha⁻¹ N was taken up by the off- and on-year plants, respectively. The difference in N uptake between on- and off-year plants may not be so great if off-year plant roots grow more and took up more N than on-year

plants, which grow in competition with fruit. This study suggests that when 'Kotata' blackberries are grown in the AY system, a split application of N in both the on-and off-year may be more efficient than a single application in one-year only.

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CHAPTER 3: NITROGEN PARTITIONING BY 'MARION' TRAILING BLACKBERRY IN ALTERNATE YEAR PRODUCTION IN POT CULTURE.

Abstract

To study the uptake and partitioning of nitrogen, 'Marion' blackberries (*Rubus* L. subspecies *Rubus* Watson) growing in the alternate year (AY) system in pot culture, were treated with either ammonium nitrate ($^{15}\text{NH}_4^{15}\text{NO}_3$) depleted in ^{15}N , or non-labeled ammonium nitrate in the spring and/or fall of 1997 and 1998. Whole plants were destructively sampled at the end of the growing season of 1997 and 1998. The majority of off-year dry weight was found in the primocanes and primocane leaves, while floricanes generally had the majority of on-year dry weight. On-year plants had a greater dry weight and N content than off-year plants. New fertilizer N was preferentially allocated to new tissues (primocanes and leaves) in both the on- and off-years. Fruit was a strong sink for new fertilizer N in the on-year. Stored N was allocated more towards the floricanes and crowns in the on-year, and crowns in the off-year. ^{15}N applied to the off-year in August resulted in higher stored ^{15}N found in the roots, crown, floricanes, and fruit, and less in the primocanes and primocane leaves the following year. Plants fertilized in both the on- and off-years had significantly more dry weight, N content, and yield, than those fertilized in one year only. Plants fertilized in only the on-year had a greater mean dry weight and yield than those fertilized only in the off-year. Plant recovery of N was not very efficient (mean = 16%, not including roots), and little applied ^{15}N remained after two growing seasons. Fertilizing 'Marion' blackberries grown in AY production in both the on- and off-years is recommended.

Introduction

Nitrogen is the most frequently deficient nutrient in crop production, so understanding its behavior is essential for maximizing agricultural productivity and reducing the impacts of nitrogen on the environment (Tisdale *et al.*, 1993). Oregon State University recommendations for trailing blackberries suggest nitrogen at 56 to 78 kg·ha⁻¹ in the spring (Hart *et al.*, 1992). However, Cortell and Strik (1997a) found a significant amount of growth of 'Marion' blackberry occurred after the late July fruit harvest, suggesting a N requirement much later in the season than previously thought.

Fruit tree shoot tissue older than two years is a common N storage site (Ludders, 1981; Titus and Kang, 1982). Yet in blackberry plants, the shoots are biennial; vegetative the first year (primocanes) and productive the second year (floricanes), after which they die, eliminating them as a possibility for long-term N storage.

Two production systems currently used to grow trailing blackberries are the alternate-year (AY) and every year (EY) systems. In the EY production system, fruit is produced every year, with primocanes and floricanes present on the plant. After harvest, the floricanes are removed and the primocanes trained onto the trellis. In the AY production system, fruit is produced every other year. Only primocanes grow in the non-productive year (off-year); these then over-winter, becoming floricanes the following year (on-year)(Strik, 1992). After harvest, all the canes are removed in October, and a new cycle begins. Usually half of the field will be in production each year. There has been little research on trailing blackberry production and physiology, especially concerning the AY production systems.

Sheets *et al.* (1975, 1987) compiled a list of advantages and disadvantages of AY production. Advantages included less labor for pruning and training, reduced disease and cold injury, lowered production costs, minimized damage to primocanes during machine harvest, and less fertilizer and pesticide inputs.

A cost study comparing AY to EY production over an eleven year period showed that EY production had an average cost of \$.88/kg, while AY was only \$.79/kg (Burt *et al.*, 1987).

In AY production, 70 to 90% of the yield of the traditional EY system is produced over a two year period (Bullock, 1963; Nelson and Martin, 1989; Sheets *et al.*, 1975). During the off-year of the AY system, blackberry produce many more primocanes than in EY production, when floricanes are present (Cortell and Strik, 1997a; Sheets and Kangas, 1970; Strik *et al.*, 1996). Nelson and Martin (1989) found 'Boysen' trailing blackberry grown in the AY system produced significantly more canes, higher yields, and smaller fruit than those grown in the EY system.

Sheets and Kangas (1970) applied nitrogen to blackberries grown in the AY system fertilized in either the on-year and off-year, or only in the on-year. They suggested there might be no advantage to fertilizing blackberries in both years, for yields were not different from when the plants received fertilizer in the on-year only. No research has been conducted to determine the importance of the timing of the nitrogen application in the AY production system.

Nelson and Martin (1986a; 1986b) did two nitrogen fertilization studies on 'Thornless Evergreen' blackberries in the EY system, showing that the rate of applied nitrogen was significantly correlated with the yield, but there was no consistent relationship of leaf nitrogen levels with yield. In a fertilization study on 'Hull Thornless' erect blackberry, Archbold *et al.* (1989) found yield was correlated with applied nitrogen. However, no correlation was found between applied N and yield in 'Arapaho' erect blackberry (Alleyne and Clark, 1997; Naraguma and Clark, 1998).

Pritts and Handley (1994) state that a split application of nitrogen is more efficient in *Rubus* spp. than a single application, but no research has been conducted on split applications in trailing blackberry in AY production. In EY production, no difference was found in the yield of 'Arapaho' thornless erect blackberry between single or split N applications (Alleyne and Clark, 1997; Naraguma and Clark, 1998).

Nitrogen-15, a stable isotope of nitrogen, has been used to research uptake and movement of N in many horticultural crops, including almonds (Weinbaum *et*

al., 1984), citrus trees (Feigenbaum *et al.*, 1987), apple trees (Grasmani and Nicholas, 1971), grapes (Hanson and Howell, 1995), pears (Sanchez *et al.*, 1991), blueberries (Retamales and Hanson, 1989), and semi-erect blackberries (Malik *et al.*, 1991) but there has been no research on trailing blackberries using nitrogen isotopes. Trailing blackberries have a very different growth habit than semi-erect types (Strik, 1992).

The objectives of this study were to develop a better understanding of the effect of AY production on nitrogen uptake and partitioning in 'Marion' trailing blackberries, and observe how the timing of fertilizer application affects nitrogen uptake and partitioning, specifically to:

- determine the influence of time of year of nitrogen fertilizer application on nitrogen partitioning and remobilization in 'Marion' blackberry plants in AY production,
- determine the influence of single or split applications of nitrogen fertilizer on 'Marion' blackberry plants in AY production,
- determine if 'Marion' blackberries require nitrogen fertilization in both the on- and off-years, or only one.

Materials and Methods

Two-year old 'Marion' blackberries grown in pot culture at the North Willamette Research and Extension Center, Aurora, Ore. were used. In 1996, the year prior to the experiment, the one-year old plants were grown in 3.8-liter pots in a greenhouse mix containing: 125 cm³ partially decomposed bark, 250 cm³ quatama soil (fine-loamy, mixed mesic Aquatic Haploxeralfs), 42 cm³ peat, 567 g dolomite, 567 g agricultural lime, 567 g gypsum, and 340 g Micromax (Scott's, Marysville, Ohio). Plants received 2 g Osmocote (Scott's, Marysville, Ohio) slow-release fertilizer per pot in June, and were watered twice daily with an overhead irrigation system. The plants were fertilized once weekly with 0.5 g Peter's (20-20-20; St.

Louis, Mo.) per liter of water until the end of the growing season. In order to have both "on-year" (fruiting) and "off-year" (vegetative) plants concurrently in the alternate year (AY) system, a portion of the one-year old off-year blackberries were cut back to the crown in October, 1996. In November, the potted plants were moved into a plastic covered hoophouse for winter protection, where they were watered once weekly, by hand. In mid-March, 1997, plants were transplanted into 7.6-liter containers, placed outdoors, and fertilized with 2.5 g slow-release phosphorous and 4.3 g slow-release potassium per pot. In February, 1998, the plants were transplanted into 19-liter containers in order to accommodate growth.

In March, May, and Aug. of both 1997 and 1998, the blackberry plants were treated with single and split applications of 6 g N in the form of either labeled ammonium nitrate depleted in ^{15}N (0.05 atom % ^{15}N) or non-labeled ammonium nitrate, as indicated in Table 3-1.

Table 3-1. Nitrogen type and timing treatments applied to 'Marion' blackberry in 1997 and 1998.

Trt. #	Nitrogen application ^z		Timing ^y
	1997	1998	
1-3	^{15}N applied, on-year	NA ^x	A
4-7	^{15}N applied, off-year	NA ^x	B
8-10	^{15}N applied, on-year	N applied, off-year	A
11-13	N applied, on-year	^{15}N applied, off-year	A
14-16	^{15}N applied, on-year	No N applied, off-year	A
17-19	^{15}N applied, off-year	N applied, on-year	A
20-22	N applied, off-year	^{15}N applied, on-year	A
23-25	No N applied, off-year	^{15}N applied, on-year	A
26-29	^{15}N applied, off-year	No N applied, on-year	B
30-33	N applied, off-year	^{15}N applied, on-year	B

^zA total of 6 g N was given to plants in each year; split applications totaled 6 g for the year.

^yApplication dates: A – single N application in March or May or split in March/May. B – single N application in August or split in March/August, May/August, or March/May/August.

^xDestructively harvested in 1997.

There were 33 treatments, with three single plant replicates per treatment. Plants were arranged in a completely randomized design. On each of the application dates, the labeled or non-labeled ammonium nitrate fertilizers were dissolved in 250 ml water, and poured directly into the pots.

At the end of the growing season, 7 October 1997, three single plant replicates for each N treatment 1 through 7 were destructively sampled. The plants were partitioned into roots, crown, primocanes, primocane leaves, floricanes, and laterals. Plant total dry weights excluded the roots, as only a subsample of roots could be taken. The separated tissues were air-dried at 60°C to a constant dry weight. Canes were cut into lengths approximately 2-3 inches. Separated tissues were mixed in large paper bags, and random pieces sampled (total of 50-100 g per tissue). The subsamples were oven air-dried at 60° C to a constant dry weight, and finely ground to pass a 40-mesh (0.6 mm) screen. Subsamples were analyzed for concentration of N and ¹⁵N by mass spectrometry at Isotope Services (Los Alamos, NM). Atom percent values were converted to the proportion of the nitrogen derived from the fertilizer (NDFF), as described by Sanchez *et al.*, (1990; adapted from Hauck and Bremner, 1976):

$$\text{NDFF} = \frac{(^{15}\text{N}_{\text{natural abundance}}) - (\text{atom } \% ^{15}\text{N})_{\text{tissue}}}{(^{15}\text{N}_{\text{natural abundance}}) - (\text{atom } \% ^{15}\text{N})_{\text{fertilizer}}} ;$$

where ¹⁵N natural abundance was considered equal to 0.36 atom percent (Hauck and Bremner, 1976).

At the end of the growing season of the second year of the study, 16 October 1998, three single plant replicates of each N treatment 8 through 33 were sampled and analyzed as described for 1997.

Throughout the harvest seasons of both years, total fresh yield data were collected. Fruit were freeze-dried to measure total yield dry weight, then ground and analyzed as described for the other tissues.

An analysis of variance was used to compare concentrations of N and NDFF of the means of the three replications of each tissue (Systat Version 7.0, SPSS Inc., Evanston, IL 1997). Dry weight, N content, and NDFF were transformed to a percentage of the total dry weight to determine allocation differences.

Results and Discussion

Unfortunately, 'Marion' blackberries did not seem suited to pot culture, as 21% of the plants died by the end of the two-year experiment (Table 3-2). Some failed to emerge after the 1997/1998 winter season, and some died possibly due to stresses from drought, cane disease, or insufficient nitrogen. A large percentage of death occurred in plants that received fertilization in March as compared to other months (Table 3.2). Twenty-nine percent of the plants that received single applications died, and 17% of those that received split applications died. No differences in percent death were observed when comparing plants that received N in one year or both, or if they received N in August or not.

Sheets *et al.* (1975, 1987) found blackberries growing in the AY production system had less disease than those growing in the EY system, but 37% of the plants in this experiment had leaf spot (*Septoria rubi* Westend).

Generally, plants suffering from a nitrogen deficiency have a lower tolerance to diseases and pests (Marschner, 1995). On 2 September 1998, leaf damaged plants were counted. Most of the plants with leaf spot also had leaf chlorosis, and a greater incidence of the disease was found in plants that received fertilizer in only one year. Off-year plants fertilized in both years had no leaf spot compared to 56% of the off-year plants fertilized in only the on-year (Table 3-2). Thus the incidence of leaf spot was apparently greater in N-deficient plants.

Marschner (1995) states that plants with a heavy fruit load are more sensitive to inadequate nutrients. On-year 'Marion' had higher dry weights and N uptake, and along with fruit N demand, most likely required higher amounts of N

Table 3-2. 'Marion' blackberry plant survival and incidence of leaf spot (*Septoria rubi* Westend).

Y ^v	Trt	Nitrogen application ^z		Timing ^y	S ^x	LS ^w
		1997	1998			
'97	1	¹⁵ N, on-year	NA ^u	March	3	NA
	2	¹⁵ N, on-year	NA	May	3	NA
	3	¹⁵ N, on-year	NA	March/May	3	NA
	4	¹⁵ N, off-year	NA	August	3	NA
	5	¹⁵ N, off-year	NA	March/Aug.	2	NA
	6	¹⁵ N, off-year	NA	May/Aug.	3	NA
	7	¹⁵ N, off-year	NA	March/May/Aug	1	NA
'98	8	¹⁵ N, on-year	N, off-year	March	3	0
	9	¹⁵ N, on-year	N, off-year	May	3	0
	10	¹⁵ N, on-year	N, off-year	March/May	3	0
	11	N, on-year	¹⁵ N, off-year	March	1	0
	12	N, on-year	¹⁵ N, off-year	May	2	0
	13	N, on-year	¹⁵ N, off-year	March/May	3	0
	14	¹⁵ N, on-year	No N, off-year	March	3	1
	15	¹⁵ N, on-year	No N, off-year	May	3	2
	16	¹⁵ N, on-year	No N, off-year	March/May	3	2
	17	¹⁵ N, off-year	N, on-year	March	1	1
	18	¹⁵ N, off-year	N, on-year	May	2	0
	19	¹⁵ N, off-year	N, on-year	March/May	2	2
	20	N, off-year	¹⁵ N, on-year	March	1	1
	21	N, off-year	¹⁵ N, on-year	May	2	1
	22	N, off-year	¹⁵ N, on-year	March/May	3	1
	23	No N, off-year	¹⁵ N, on-year	March	1	1
	24	No N, off-year	¹⁵ N, on-year	May	2	0
	25	No N, off-year	¹⁵ N, on-year	March/May	2	0
	26	¹⁵ N, off-year	No N, on-year	Aug	3	2
	27	¹⁵ N, off-year	No N, on-year	March/Aug..	2	3
	28	¹⁵ N, off-year	No N, on-year	May/Aug.	2	2
	29	¹⁵ N, off-year	No N, on-year	March/May/Aug	3	3
	30	N, off-year	¹⁵ N, on-year	Aug.	3	2
	31	N, off-year	¹⁵ N, on-year	March/Aug.	2	1
	32	N, off-year	¹⁵ N, on-year	May/Aug.	3	2
	33	N, off-year	¹⁵ N, on-year	March/May/Aug	2	2

^zA total of 6 g N was given to plants in each year; split applications totaled 6.

^yApplication dates: March, May, Aug. = N application in that month only; March/May, March/Aug., May/Aug., March/May/Aug. = split applications in months indicated.

^xSurviving plants from three replications

^wPlants with leaf spot.

^vYear plants were sampled in.

^uPlants destructively sampled October 1997.

than off-year plants. As supporting evidence for this higher demand, 67% of the on-year plants had high infestations of leaf spot as compared to only 20% of the off-year plants.

Timing of N application can be an important factor in plant disease resistance or susceptibility (Marschner, 1995). When winter wheat received a fall application of N, the incidence of take-all disease (*Gaeumanomyces graminis*) was greatly increased, and yield dramatically decreased when compared to the same amount of N applied in the spring (MacNish, 1988). When on-year blackberry plants were fertilized in both years, 58% of the plants whose fertilization included an August application had leaf spot, while 33% of those that received N in March or May or March/May had leaf spot. Eighty-three percent of on-year plants that received fertilizer only in the off-year of 1997, which included August fertilization, had leaf spot. A split application reduced disease levels and increased yield in wheat (Darwinkel, 1980a and b), but this effect was not observed in blackberry.

Off-year 1997

Off-year treatments (4-7) consisted of a total of 6 g labeled N applied in March/Aug (split 3 g N each month), May/Aug (split 3 g N each month), March/May/Aug (split 2 g N each month) and August (6 g N). Two of the three replications in the March/May/Aug treatment died, and therefore this treatment could not be included in statistical analyses. None of the following parameters were significant using ANOVA, ($P=0.05$), thus trends are mentioned here.

Off-year plant total dry weight averaged 93.8 g per plant, with 55% in primocane leaves, 36% in primocanes, and 10% in the crown, with no difference in allocation among the N timing treatments (Table 3-3). Plants treated with a split application in May/August contained the highest mean total and individual tissue dry weights.

Plants treated with a single August application tended to have the highest N concentration in all tissues and the split May/Aug application the lowest (Table 3-3). Plants averaged a total N accumulation of 1484 mg, with the May/Aug treatment having the highest and March/Aug the lowest. Seventy-two percent of the plant N was found in the primocane leaves, with 25% in the primocanes, and 3% in the crowns. The May/August timing had the highest mean N content in the primocanes, primocane leaves, and total plant, but the crowns in the August treatment had a higher mean than the May/August, or March/August treatments.

An average of 42% of the N in the roots and crowns was NDFF, and NDFF of primocanes and primocane leaves averaged 61%. No differences in allocation of NDFF in the tissues were measured among treatments.

The May/August treatment had the highest NDFF in primocane leaves and the total plant, but the crowns in the single August treatment had a higher mean than the May/August, or March/August treatments. Root %NDFF was also higher in the single August treatment. This suggests the possibility that N applied late in the season was allocated to storage tissue; the roots and crowns. Post-harvest applications of N to pears also resulted in allocation of the fertilizer N to the roots (Sanchez, et al., 1990 and 1992). Blueberries fertilized with N in August or September allocated a greater percentage of fertilizer N to the roots than plants that were treated in May or June (Throop and Hanson, 1997). Autumn uptake of N also contributed to storage tissues in apples (Millard and Thompson, 1989).

Plants averaged a total of 908 mg NDFF, with 73% of the NDFF in the plant found in the primocane leaves, 25% in the primocanes, and 2% in the crown. Excluding roots, 15% of the ^{15}N was recovered in these off-year plants by October. Perhaps N was leached from the pots because this value is low compared to field-grown off-year 'Kotata' blackberry plants, which had 30% N recovery, excluding roots (see Chapter 2). Typical fertilizer N recovery in crop plants is 25-50% (Weinbaum et al., 1992). Fertilizer N recovery was reported at 15-20% for pears (Sanchez et al., 1991) and 7-11% for grapes (Hanson and Howell, 1995).

Table 3-3. Effect of nitrogen application in the off-year of 'Marion' blackberry on various parameters in 1997 (n=3).

Treatment no.		4	5	6
		August	March/Aug	May/Aug
Dry weight (g)	Crown	3.7	2.6	3.9
	Primocane	29.4	29.5	47.6
	P. leaves	50.5	47.6	66.5
	Total	83.6	79.7	118.0
N concentration (%)	Roots	1.5	1.4	1.3
	Crown	1.3	1.2	1.2
	Primocane	1.2	1.1	0.9
	P. leaves	2.0	1.8	1.9
N content (mg)	Crown	52.4	30.4	48.3
	Primocane	376.4	317.1	415.9
	P. leaves	1044.8	913.9	1252.2
	Total	1473.7	1261.4	1716.3
NDFF (%)	Roots	46.4	44.5	43.5
	Crown	41.2	39.2	40.7
	Primocane	63.4	60.8	60.3
	P. leaves	59.4	59.0	62.8
NDFF (mg)	Crown	22.2	12.2	19.9
	Primocane	246.3	199.3	249.8
	P. leaves	630.3	557.2	786.2
	Total	898.8	768.7	1055.8

On-year 1997

On-year treatments (1-3) consisted of a total of 6 g labeled N applied in March, or May, or March/May (3 g N each month). Floricane leaves had all senesced by the October sampling date, and were not included in the analysis. Few significant effects were found by ANOVA, thus, trends are mentioned here unless otherwise indicated.

On-year plants averaged 114 g dry weight per plant. The primocanes, primocane leaves, and floricanes each accounted for an average of 30.5% of the total dry weight, and the crowns only 4% (Table 3-4). Total plant dry weight was not affected by treatment, but the partitioning of the dry weight was. Plants with a split application in March/May allocated significantly more dry weight to the floricanes (51%) than the other timings of March at 16% ($p=0.011$) and May at 22% ($p=0.024$).

Floricanes and primocanes contained the lowest average N concentration (0.7%), and primocane leaves contained the highest (1.3%)(Table 3-4). The March/May application led to the highest %N in all tissues, but was significantly so only in the primocanes, where the May treatment was lower than the March treatment ($p=0.006$) and the March/May treatment ($p=0.001$). Plants averaged a total of 1077.4 mg N in vegetative tissues, with no differences among treatments. The majority of the N was found in the primocane leaves (51%) with floricanes and primocanes in the middle (23% each), and crowns with the lowest (3.3%). The March/May fertilized plants allocated significantly more N to the floricanes than the single March or May applications ($p=0.013$ and $p=0.036$, respectively).

Floricanes contained the lowest mean concentration of NDFF (25.6%), and primocanes and primocane leaves contained the highest (38.2 and 35%, respectively). Pot-grown 'Chester' Thornless' blackberry fertilizer N patterns were similar (Malik *et al.*, 1991). There were no differences among treatments. Plants took up an average of 387 mg total of fertilizer nitrogen in the vegetative tissues, and 98 mg in the fruit, totaling 485 mg NDFF. Fertilizer N recovery for on-year plants was only 8%, half that of off-year plants, and much less than field grown 'Kotata' which had 30% recovery (see Chapter 2). Primocane leaves contained 58% of the NDFF, with primocanes and floricanes averaging 20%, and crowns 3%.

Treatments 1-3 and 8-16 were harvested from the beginning of July to mid-August. Using ANOVA, no parameters were significant $P<0.05$, and a t-test between any single vs any split application showed no significance. Deletion of possible outliers (plants with only one or two berries), and transformation of the fruit weight to a percentage of the total plant dry weight showed no further insight, therefore trends are discussed here. The 'Marion' plants averaged 42.5 g fresh

Table 3-4. Effect of nitrogen application in the on-year of 'Marion' blackberry on various parameters in 1997 (n=3).

Trt. No.		1	2	3
		March	May	March/May
Dry Weight (g)	Crown	3.0	4.5	3.3
	Primocane	40.9	41.9	23.0
	P. leaves	49.1	42.3	30.8
	Florican	18.0	25.2	60.3
	Total	111.0	113.9	117.5
% N	Roots	1.07	0.97	1.35
	Crown	0.92	0.86	1.23
	Primocane	0.74	0.60	0.79
	P. leaves	1.28	1.31	1.42
	Florican	0.61	0.73	0.76
N content (mg)	Crown	29.3	39.7	38.3
	Primocane	302.5	250.5	184.0
	P. leaves	654.8	552.2	443.1
	Florican	105.0	183.4	449.6
	Total	1091.7	1025.7	1114.9
% NDFF	Roots	28.6	34.5	33.6
	Crown	27.8	31.1	28.4
	Primocane	25.0	42.0	38.0
	P. leaves	34.5	43.6	36.6
	Florican	25.9	25.5	25.5
NDFF (mg)	Crown	8.9	12.4	11.3
	Primocane	62.6	104.3	74.9
	P. leaves	260.8	241.6	173.0
	Florican	27.5	49.8	134.8
	Total	360.0	408.0	394.0

yield (9.4 g dry mass) per plant, with a mean fruit weight of 2.0 g (Table 3-5). Fruit weight was much less than the average fruit weight for field-grown 'Marion' blackberries of 5 g, likely a reflection of plant stress (Bell *et al.*, 1995; Cortell and Strik, 1997b; Strik, 1996). Mature 8 year-old 'Marion' grown in the field without floricanes the previous year averaged between 9 and 17 kg fruit per plant (Cortell and Strik, 1997b). In this study, nitrogen in fruit averaged 1.9%, or 187 mg per plant, and the NDFF averaged 50%, or 98 mg per plant. Fruit contained 20% of the NDFF found in the on-year plants.

The split March/May application had the highest mean fresh yield, dry yield weight, average fruit weight, and N content. The single application in May led to the highest mean percent and NDFF (Table 3-5). When comparing any split application to any single application, fresh and dry fruit weight and berry size in the split application tended to be greater than in the single application (Table 3-5).

Table 3-5. Effect of nitrogen application on yield and nitrogen partitioning to fruit of 'Marion' blackberry, 1997 (n=33, except for NDFF parameters, where n=25).

Time of Application	Total Fresh Yield (g)	Yield dry weight (g)	Fruit Weight (g)	Fruit N (%)	Fruit N content (mg)	Fruit % NDFF	Fruit NDFF (mg)
March	39.9	9.0	1.8	1.8	170.6	47.5	97.3
May	40.8	8.5	1.9	2.1	181.3	55.5	102.9
March/May	46.8	10.4	2.2	1.8	204.6	47.2	93.3
Single	40.3	8.8	1.8	2.0	176.0	51.5	100.1
Split	46.8	10.4	2.2	1.8	204.6	47.2	93.3

Off-year 1998

There were nine treatments (8-16) applied to the off-year plants sampled in 1998 (Table 3-6). Few significant effects were found by ANOVA, thus, trends are mentioned here unless otherwise indicated.

In 1998, off-year total plant growth (excluding roots) averaged 110 g (Table 3-6). Total growth was 16 g more than in the 1997 off-year, but proportions were similar.

Out of the different months in which N was applied, the May application led to the greatest mean total dry weight. Plants fertilized in both years all had significantly more dry weight (3 times as much) than those fertilized in the on-year only ($P=0.000$, Table 3-6). No significant differences were found among any split and single applications, or among the different months of application.

Primocane leaves generally had the highest N concentration, averaging 1.6%, with primocanes at 1.4%, and crowns and roots at 1.3%. When plants were fertilized in both years, the March application had a significantly lower N concentration in all tissues than May or March/May fertilization (Table 3-6).

An average of 723 mg N was lost from these plants when the floricanes, primocanes, and primocane leaves were removed in October for AY production in 1997 (Table 3-4). Excluding the roots, this accounted for 67% of the N in the plant, leaving N only in the roots and crown as reserves for the next year. In pot-grown 'Chester Thornless' blackberries a majority of dry weight and N was found in the roots (Malik *et al.*, 1991), so root N reserves were likely high in this study also. Off-year plant N content in 1998 ranged from 0.4 g to 2.6 g per plant (Table 3-6).

Nitrogen content in plants treated in both years followed the same trend as dry weight, where the May treated plants tended to have the most N, and the March treated plants the least (Table 3-6). However, in the on-year only treatments, the March application had a slightly higher amount of N. When looking at allocation patterns, N followed the same trend as dry weight, with plants receiving N in both years allocating more N to the primocanes, whereas plants receiving N in only the on-year allocated more to the crown (Table 3-6).

NDFF was highest in plants treated with N in both years, with the ^{15}N applied in the second year, 1998 (Table 3-6). May applications consistently contained the highest NDFF, and March the lowest. Plants treated with N in both years with the ^{15}N applied in the 1997 off-year had a slightly higher mean NDFF than those

Table 3-6. Effect of nitrogen application in the off-year of 'Marion' blackberry on various parameters in 1998.

1997 1998		¹⁵ N (on-year) N (off-year)			N (on-year) ¹⁵ N (off-year)			¹⁵ N (on-year) None (off-year)		
Trt. No.		8	9	10	11	12	13	14	15	16
Tissue		March	May	March/ May	March	May	March/ May	March	May	March/ May
Dry weight (g)	Crown	8.5	7.2	6.2	8.4	14.4	4.3	4.1	6.0	5.8
	Primocane	40.7	49.5	43.5	35.6	48.4	24.8	8.7	11.4	7.9
	P. leaves	64.5	62.6	63.8	34.1	67.6	38.1	18.4	16.7	17.7
	Total	113.6	119.4	113.5	78.1	130.4	67.2	31.1	34.0	31.4
N conc. (%)	Roots	0.7	1.7	1.8	0.9	2.0	1.9	0.8	0.8	0.8
	Crown	0.8	1.7	1.7	1.8	1.6	1.6	0.9	0.9	0.9
	Primocane	0.7	2.1	1.8	1.0	1.7	2.1	0.9	0.9	0.9
	P. leaves	0.9	2.2	2.1	1.1	2.3	1.5	1.5	1.3	1.4
N (mg)	Crown	71	133	108	154	232	68	36	53	54
	Primocane	267	953	776	365	834	530	80	98	72
	P. leaves	570	1342	1354	379	1547	567	277	204	243
	Total	908	2427	2238	897	2613	1164	390	355	369
NDFF (%)	Roots	15.6	6.9	8.0	49.5	65.2	64.1	20.1	23.8	19.4
	Crown	17.0	8.6	10.4	55.2	64.5	49.2	19.1	22.6	17.8
	Primocane	6.3	2.4	2.6	69.9	77.7	81.6	10.8	13.7	11.8
	P. leaves	5.2	2.2	2.3	67.9	79.0	27.5	10.6	14.2	11.8
NDFF (mg)	Crown	13	13	12	85	150	33	7	12	11
	Primocane	17	25	20	255	648	432	9	14	8
	P. leaves	29	31	31	257	1222	156	29	28	28
	Total	59	69	63	597	2020	622	44	54	47

that received ^{15}N only in the on-year. When comparing allocation patterns between treatments, no difference was found in the crowns, but plants treated in both years allocated more NDFF to the primocanes, and less to the primocane leaves.

An average of 377 mg NDFF was lost from these plants when the floricanes, primocanes, and primocane leaves were removed for AY production in October 1997 (Table 3-4). Excluding the roots, this accounted for 97% of the N in the plant, leaving N only in the roots and crown as reserves for the next year. An average of only 11 mg NDFF remained in the crown as storage for the 1998 season. In 'Chester Thornless' blackberries, roots were a major N storage site (Malik *et al.*, 1991). This supports remobilization of N from the roots to account for the higher NDFF levels of 44 to 69 mg in the crowns, primocanes, and primocane leaves of the 1998 off-year plants.

Off-year roots were dependent on new fertilizer N, as 60% of the N in the roots was from newly applied fertilizer (trts. 11-13), and 15.6% was stored ^{15}N applied the year before (trts. 8-9 and 14-16; Table 3.6).

A large amount of N was lost in 1997 to fruit harvest (97.8 mg) and removal of floricanes, primocanes, and primocane leaves (376.5 mg). After two seasons, the 'Marion' plants, excluding the roots, retained 12% of the ^{15}N initially acquired by the plant. In comparison, 'Chester Thornless' had 27% of the N that was initially acquired by the plant, of which roots contained more than half (Malik *et al.*, 1991).

On-year 1998

There were 17 different nitrogen treatments (17-33) applied to the on-year plants sampled in 1998 (Table 3-7). Due to an inadequate number of surviving replications, treatments 17-21 and 23-25 were not included in statistical analyses. Few significant effects were found by ANOVA, thus, trends are mentioned here unless otherwise indicated.

In 1998, on-year total plant dry weight (excluding roots) averaged 125 g, 11 g more than the 1997 on-year, but allocations were similar. Most of the florican leaves had senesced by the sampling date.

Table 3-7. 1998 'Marion' on-year treatments (17-33).

Fertilizer treatment			
Trt #	1997 (off-year)	1998 (on-year)	Month of application
17	¹⁵ N applied, off-year	N applied, on-year	March
18	¹⁵ N applied, off-year	N applied, on-year	May
19	¹⁵ N applied, off-year	N applied, on-year	March/May
20	N applied, off-year	¹⁵ N applied, on-year	March
21	N applied, off-year	¹⁵ N applied, on-year	May
22	N applied, off-year	¹⁵ N applied, on-year	March/May
23	No N applied, off-year	¹⁵ N applied, on-year	March
24	No N applied, off-year	¹⁵ N applied, on-year	May
25	No N applied, off-year	¹⁵ N applied, on-year	March/May
26	¹⁵ N applied, off-year	No N applied, on-year	Aug
27	¹⁵ N applied, off-year	No N applied, on-year	March/Aug..
28	¹⁵ N applied, off-year	No N applied, on-year	May/Aug.
29	¹⁵ N applied, off-year	No N applied, on-year	March/May/Aug
30	N applied, off-year	¹⁵ N applied, on-year	Aug.
31	N applied, off-year	¹⁵ N applied, on-year	March/Aug.
32	N applied, off-year	¹⁵ N applied, on-year	May/Aug.
33	N applied, off-year	¹⁵ N applied, on-year	March/May/Aug

Plants fertilized in both years (trts. 17-22 and 31-33) tended to have an average total dry weight of 130 g, which was greater than plants that received fertilizer only in the on-year (110 g), or only in the off-year (70 g)(Table 3-8). In plants fertilized in both years, the split application led to a higher mean total dry weight (136 g), than the single application (120 g), and August fertilized plants tended to have a slightly higher mean (133 g) than other months (123 g). There were no consistent differences when comparing March, May, and March/May.

Plants treated with N in only the off-year (1997), which included split August treatments, had the lowest concentration of N in all tissues (Table 3-8). Plants treated in both years with split August treatments and plants treated in only the on-

year (1998) had the highest concentration of N. There were no consistent differences when comparing the time of application. However, plants fertilized in both years had a significantly higher N content (1979 mg) than those fertilized in the on- or off-year only (1853 and 633 mg, respectively). There was no difference among the means when comparing all split applications with all single applications. The May application consistently had the highest N content, and March the lowest (Table 3-8). When plants were fertilized in both years, those including an August treatment had a higher mean N content (2264 mg) than those without (1688 mg). Plants that received N in August received N two months before the sampling date, so higher N values would be expected.

In fall, 1998, the NDFF concentration and content was lowest in the treatments where ^{15}N was applied only in 1997 (trts. 17-19 & 26-29). NDFF in these treatments represents stored ^{15}N from fertilizer applied in 1997. Treatments where N was applied in both years (17-19) had higher N content values and fruit yield, but treatments where N was applied in August (26-29) had higher total stored NDFF values.

Treatments (17-22 & 26-29) lost an average of 34.4 mg stored NDFF in harvested fruit in 1998 (Table 3-9), which was 16.5% of the total stored NDFF found in the plant. By the end of the 1998 season, plants retained only 2.9% of the ^{15}N applied in 1997 (excluding roots).

Roots were dependent on new fertilizer N, which accounted for 65.4% of the N found in the root (trts. 20-25). Twelve percent of the on-year root N was from stored ^{15}N applied the previous season (17-19), which doubled when they were fertilized in the previous August (trts. 27-29). This suggested August applied N was allocated to the roots as was observed in pears (Sanchez *et al.*, 1990 & 1992), blueberries (Throop and Hanson, 1997), and apples (Millard and Thompson, 1989).

Table 3-8. Effect of nitrogen application in the on-year of 'Marion' blackberry on various parameters in 1998.

		¹⁵ N - 1997 (off-year) N - 1998 (on-year)			N - 1997 (off-year) ¹⁵ N - 1998 (on-year)			none - 1997 (off-year) ¹⁵ N - 1998 (on-year)			¹⁵ N - 1997 (off-year) none - 1998 (on-year)				N - 1997 (off-year) ¹⁵ N - 1998 (on-year)			
		March/ March/			March/ March/			March/ March/			March/ March/				March/ March/			
Tissue		March	May	May	March	May	May	March	May	May	Aug	March/ Aug	May/ Aug	May/ Aug	Aug	March/ Aug	May/ Aug	May/ Aug
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Dry weight (g)	Crown	5.8	7.2	11.1	1.9	5.2	6.0	5.8	7.1	6.2	5.1	5.8	5.1	4.4	4.7	9.1	6.1	6.6
	Primocane	38.9	27.2	43.3	33.0	50.6	28.2	22.2	58.8	34.7	8.8	4.1	3.6	6.9	16.7	31.5	42.4	31.1
	P. leaves	39.7	44.2	49.5	51.4	47.6	22.2	14.2	58.9	42.6	18.0	9.9	13.2	17.7	28.1	40.8	46.7	36.3
	Florican	43.5	34.2	39.4	4.5	40.4	36.9	42.7	24.2	6.1	42.3	38.3	39.1	38.3	39.2	58.0	54.4	50.2
	F. leaves	26.5	0.7	9.0	0.0	0.0	1.8	0.0	5.7	1.8	1.8	9.9	5.2	3.6	6.7	15.6	0.0	5.9
	Total	154	114	152	91	144	95	85	155	91	76	68	66	71	95	155	150	130
N concentration (%)	Roots	0.9	1.8	1.2	1.2	1.4	1.8	1.9	1.8	1.7	0.9	0.9	0.9	0.9	1.7	1.5	1.9	1.9
	Crown	0.9	1.4	1.4	1.2	1.5	1.8	1.7	1.8	1.6	1.1	1.0	1.1	0.9	1.6	1.9	1.8	1.7
	Primocane	0.8	2.0	1.0	1.1	1.67	1.8	1.5	1.4	1.6	0.8	0.9	0.9	1.0	1.8	1.4	2.0	1.8
	P. leaves	1.3	2.0	1.5	1.7	1.8	2.0	1.7	1.9	1.8	1.2	1.3	1.7	1.4	2.1	2.3	2.4	2.1
	Florican	0.6	1.3	0.8	0.9	0.8	1.4	1.6	1.8	1.2	0.8	0.7	0.7	0.6	1.3	1.2	1.2	1.4
	F. leaves	1.0	2.1	1.5	na	na	1.4	na	2.4	1.7	1.0	1.0	1.0	0.9	1.7	1.7	na	1.6
N content (mg)	Crown	51	101	154	23	78	104	98	127	99	56	53	54	41	75	177	111	121
	Primocane	321	530	430	350	845	490	341	841	543	72	36	31	64	294	457	846	494
	P. leaves	529	891	722	892	865	445	247	1128	773	224	122	207	250	588	961	1119	787
	Florican	258	427	321	41	328	491	696	430	71	330	281	250	235	498	723	633	711
	F. leaves	266	14	136	na	na	73	na	135	30	51	94	106	51	165	259	na	92
	Total	1424	1963	1763	1305	2116	1555	1382	2661	1516	699	585	595	625	1565	2577	2709	2205
NDF concentration (%)	Roots	9.5	15.8	11.2	60.6	63.0	64.7	70.4	65.9	68.0	27.7	16.2	21.0	31.0	50.2	58.8	59.8	61.5
	Crown	8.1	13.9	14.3	61.9	50.8	60.9	59.2	61.6	55.9	30.0	23.2	28.8	31.7	41.0	45.0	55.8	45.9
	Primocane	6.2	6.0	3.5	68.8	75.7	77.2	74.5	75.8	76.7	29.2	19.4	23.9	33.0	69.0	75.7	74.6	75.3
	P. leaves	2.2	4.0	3.1	68.5	76.0	76.4	73.7	79.0	76.7	27.1	17.1	22.5	25.4	52.0	76.3	78.5	78.3
	Florican	7.8	19.3	15.4	59.0	24.6	68.8	65.9	61.2	66.4	52.5	35.4	46.1	44.6	47.7	45.9	30.1	56.5
	F. leaves	2.3	5.3	5.0	na	na	11.3	na	9.1	9.6	23.2	29.2	27.9	27.4	18.7	12.2	na	12.0
NDF content (mg)	Crown	4	14	22	14	40	64	58	78	55	18	13	16	13	31	83	64	57
	Primocane	20	32	15	241	640	379	254	638	416	21	6	8	21	201	345	633	369
	P. leaves	12	35	22	611	657	342	182	891	593	59	20	52	65	318	738	877	625
	Florican	20	83	49	24	81	338	459	263	47	173	121	115	116	229	376	200	402
	F. leaves	6	1	7	na	na	52	na	104	23	19	18	26	13	83	178	na	63
	Total	62	164	116	890	1417	1139	953	1974	1134	276	178	204	224	834	1719	1774	1515

Only 4.8% of the new fertilizer NDFF in the plant was allocated to the crowns, suggesting crowns are not as dependent on new N as new growth (trts. 21-25 & 30-33). Since roots and crowns have been reported to be N storage sites, perhaps if N had been sufficient, root and crown NDFF values would have been higher.

The March, May, and March/May treatments that received ^{15}N in 1998 had the highest mean NDFF content (Trts. 20-25 & 31-33; Table 3-8). Out of the March, May, or March/May applications, an application in May consistently led to the greatest NDFF, and March the lowest. Plants that received ^{15}N in 1998 with a split August application (trts. 31,32 & 33) had a high mean of 1669 mg NDFF per plant, whereas the single August application (trt. 30) averaged only 834 mg NDFF per plant. When looking at remobilization of stored ^{15}N from August of 1997 (trt. 26), although fertilizer N recovery was low, plants that received a single August application retained more NDFF than the split March/Aug and May/Aug applications (trts. 27-29; Table 3-8).

The preference of new fertilizer N being allocated to new growth and stored N to the floricanes is similar to patterns observed in 'Chester Thornless' (Malik *et al.*, 1991). No large differences in dry weight, N content, NDFF, and yield were observed among plants fertilized in both years (trts. 20-22) and plants fertilized in only the on-year (23-25). But when looking at plants fertilized in only the off-year of 1997 (27-29), large differences in N content, NDFF, and yield were observed. This suggests a much higher demand for N in the on-year than the off-year, which was also observed in 'Kotata' (see Chapter 2).

Plants fertilized with ^{15}N in the on-year of 1998 (trts. 20-25), lost an average of 148 mg NDFF in the harvested fruit, and had 1251 mg in vegetative tissue by October, so 23% of the applied ^{15}N was accounted for, not including the roots. Plants whose fertilization included August (trts. 30-33) lost 151 mg in fruit, and had 1460.3 mg NDFF in vegetative tissue, so 26.9% of the applied ^{15}N was accounted for. The 1998 fertilizer N recovery values were greater than those observed in 1997 of 15.1% for the off-year, and 8.1% in the on-year.

Apple tree flowering was enhanced by autumn applied N (Delap, 1967), and late summer N applications contributed more N to apricot blossoms the following spring than an early summer application (Weinbaum *et al.*, 1980). In this study, replication was not high enough to satisfactorily compare the two treatments, but no difference was found between the mean yields of August treated plants (trts. 30-33) and those that received N only in March, May, or March/May (trts. 20-22).

The off-year plant had an average of only 249 mg in the primocanes and crown, and an unknown amount in the roots as reserves for next year's growth. Corresponding 1998 plants (trts. 26-29; Table 3-9 & 3-3) had an average of 264 mg NDFF in tissues and fruit. This value does not include stored NDFF lost in the senesced floricanes leaves, so it is conservative. In 1997, primocane N was 61.5 mg, but when these became the floricanes in 1998, they, along with the floricanes leaves and fruit they produced, contained 150.1 mg stored NDFF. The higher mean values in 1998 for stored NDFF could only have been from N remobilized from the crowns and roots, since the primocanes did not contain that amount of NDFF.

In 1998, fresh fruit yield averaged 74 g (14.8 g dry weight) per plant, with an average mean fruit weight of 1.8 g (Table 3-9). Fruit-N averaged 1.7%, or 227 mg per plant (Table 3-9).

Generally, plants with the highest fresh and dry yield received N in both years (17-21, and 31-33), and plants with the lowest yield received N only in one year (23-29)(Table 3-9). When averaging over treatments and comparing any single application to any split application, no significance was found in any yield parameter at the $P=0.10$ level. When comparing the time of application, no significance was found except in %N, where treatments in March, May, and March/May led to the highest concentration of N in fruit.

Table 3-9. Effect of nitrogen fertilization on yield and nitrogen partitioning to fruit in 'Marion' blackberry, 1998 (n=3).

Trt	Fertilization		Yield fresh weight (g)	Yield dry weight (g)	Fruit Weight (g)	Fruit %N	Fruit N content (mg)	Fruit % NDFF	Fruit NDFF (mg)
	1997 (off- year)	1998 (on- year)							
17	¹⁵ N	N	162.8	35.1	1.8	2.0	716.0	3.98	28.5
18	¹⁵ N	N	151.2	30.9	1.9	2.0	627.3	4.11	25.8
19	¹⁵ N	N	91.0	18.2	1.7	2.0	368.5	3.6	13.2
20	N	¹⁵ N	40.2	7.9	1.8	2.2	172.7	74.4	128.5
21	N	¹⁵ N	78.9	16.7	1.4	2.1	340.4	77.4	263.5
22	N	¹⁵ N	NA						
23	No N	¹⁵ N	20.7	4.5	1.3	1.9	86.4	72.7	62.8
24	No N	¹⁵ N	45.7	6.7	1.7	2.9	197.6	78.0	154.2
25	No N	¹⁵ N	52.7	8.4	2.4	2.1	179.1	73.2	131.0
26	¹⁵ N	No N	85.3	17.1	1.6	1.2	198.3	32.3	60.6
27	¹⁵ N	No N	68.0	8.9	1.4	1.1	101.1	34.0	34.4
28	¹⁵ N	No N	46.1	8.8	1.3	1.3	110.3	39.5	44.2
29	¹⁵ N	No N	45.6	7.4	1.3	1.2	88.5	38.3	34.0
30	N	¹⁵ N	61.4	12.3	1.6	1.5	174.0	57.1	98.4
31	N	¹⁵ N	74.8	16.5	1.6	2.1	325.3	61.9	199.9
32	N	¹⁵ N	120.7	23.7	1.8	1.3	307.3	NA	NA
33	N	¹⁵ N	115.3	25.7	1.5	1.8	425.0	43.3	155.2

When averaging over treatments and comparing any plants that received fertilizer in both years as compared to only in the off-year or the on-year, plants with N applications in both-years had a significantly higher fresh and dry yield. Those plants fertilized in the on-year only tended to have the highest %N, and those fertilized only in the off-year contained the lowest. Plants fertilized in the on-year only had higher yields than those fertilized in the off-year only.

When comparing plants that received fertilizer in August to those that received N only at other times, no difference was found in fresh or dry yield, but the August-treated plants had less fruit weight, concentration of N, and N content.

Summary

In the off-year, new fertilizer N was allocated to new growth (primocanes and primocane leaves) and stored N was found in higher amounts in the crown. In the on-year, new fertilizer N was allocated to the primocanes, primocane leaves and fruit, and stored N from the previous year was allocated to the floricanes and crowns. The percentage of fertilizer N was high in the roots of both on- and off-year plants, and stored fertilizer N low. The percentage of stored N in the roots was higher when ^{15}N was applied the previous fall. Most leaf N concentration values in both the on- and off-years were below the recommended 2-3% N (Hart *et al.*, 1992) suggesting a N deficiency.

Between 50% and 75% of the N in fruit was from the fertilizer (1997 and 1998, respectively). Stored ^{15}N , applied in March, May, or March/May of 1997, accounted for only 3.9% of the nitrogen in the 1998 fruit. However, stored ^{15}N applied in the fall of 1997, accounted for 28% of the N in the 1998 fruit.

Plants fertilized in both the on- and off-years had significantly more dry weight, N content, and yield than those fertilized in only one year. However, plants fertilized only in the on-year had higher dry weight and N values than those fertilized only in the off-year, illustrating a greater response for N in the on-year. Fifty-six percent of the off-year plants fertilized in only one year had leaf spot compared to none with leaf spot when fertilized in both years. New growth was highly dependent on new fertilizer N, so fertilization in both years would be recommended.

In 1998, plants fertilized in both years allocated more dry weight, N, and NDFF to the primocanes, and less to the crown than those fertilized in the on-year only. Plants fertilized in only the on-year had a strong N sink in the fruit and most likely did not have 'extra' N to store as reserves in the crown.

In on-year plants in 1997, a split application of N in March/May led to a higher mean total dry weight, N content, and fruit yield and weight than single applications in March or May. In the split application, more dry weight, N, and NDFF was

allocated to the floricanes than in the single applications. These differences between single and split applications were not observed in the 1998 on-year plants. The single May application tended to have higher N and NDFF values, and March the lowest in both 1997 and 1998. No difference was observed in incidence of disease.

On-year fertilizer N recovery averaged 8% in 1997 and 23% in 1998 (values do not include roots). Off-year plants averaged 15% recovery in 1997 and 18% in 1998. After two seasons, off-year plants retained 0.9% of the ^{15}N applied, and on-year plants retained 1.2%. Plant recovery of N was not very efficient and little applied ^{15}N remained after two growing seasons.

At the end of 1997, on-year plant floricanes and primocanes were removed for AY production. This left only 10.8 mg NDFF in the crowns, and an unknown amount in the roots as reserves for next year's growth. Therefore, remobilization would have had to occur to account for 44 to 69 mg NDFF found in the 1998 off-year plants. A similar pattern occurred between the 1997 off-year and 1998 on-year plants, where more NDFF was found the second year than remained in the crowns and primocanes at the end of the 1997 season.

The experimental conditions in this study, such as limited N supply, use of pot culture, and disease stress may have had significant effects on plant growth, and N uptake, partitioning and remobilization. However, the data show a difference in allocation of new and storage N, and indicate that remobilization of N occurred in the plant.

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CHAPTER 4: CONCLUSIONS

The purpose of this research was to characterize nitrogen partitioning and remobilization in 'Marion' and 'Kotata' blackberries in the AY system. What is the influence of time of year of N application? Is there a difference between single or split N applications? And do blackberries grown in the AY system require N in both the on- and off-years, or only one year? The following is a summary of findings.

'Marion' and 'Kotata' had similar dry weight and N allocation patterns. The majority of off-year dry weight accumulation was found in the primocanes and primocane leaves, while floricanes generally had the majority of on-year dry weight accumulation. On-year plants had a greater dry weight and N content than off-year plants. New fertilizer N was preferentially allocated to the primocanes and primocane leaves in both the on- and off-years. Fruit was a strong sink for new fertilizer N in the on-year. Stored N was found in the floricanes and crowns in the on-year, and crowns in the off-year.

'Marion' plant recovery of fertilizer ^{15}N was low, averaging 16% in on-year plants, and 17% in off-year plants by the end of the first growing season (not including root N). 'Kotata' plant recovery was much higher, averaging 63% fertilizer ^{15}N recovery in on-year plants, and 30% in off-year plants. After two seasons, an average of only 1.1% of the applied ^{15}N remained in 'Marion' plants. On-year 'Kotata' plants retained 18.7% of the applied ^{15}N , and off-year retained 8.2% by the end of two seasons. The differences in recovery between 'Marion' and 'Kotata' could have been a result of the different ages of the plants ('Marion' were 2 year-old plants, 'Kotata' were mature) or growing conditions (pot vs. field-grown).

Primocanes, primocane leaves, floricanes, and fruiting laterals that were removed from the on-year 'Kotata' plants in October of 1997 for AY production contained an average of 73% of the N content, and 82.8% of the NDF that remained in the plant by this time (not including roots). Unless the pruned canes are left in the field for N recycling, a large amount of N would be lost. Fruit were another

large loss, taking an average of 24.8 g N. In 1997, fruit contained 7.6 g NDFF, 38% of the applied ^{15}N that was acquired by the plant. In 1998, fruit contained 4.5 g stored ^{15}N .

It is important to apply N as close as possible to the time of demand by the plant to optimize N use and to reduce the possibility of groundwater contamination. Total dry weight, N content, and NDFF increased in 'Kotata' blackberries at least through July, indicating that a split application would be much more efficient than a single application early in the season. In 'Marion', plants that received N in May (single May application, or split with March) consistently tended to have a higher dry weight, N content, and NDFF than plants that received N only in March.

In 1997, off-year 'Marion' plants were fertilized in March/Aug, May/Aug, and August. By October, the single August treatment (which had received N most recently) produced the highest % N in all tissues, but the split May/August application led to the highest total dry weight, N and NDFF. In 1998, on-year 'Marion' plants whose fertilization in the off-year included August, retained a higher mean N, NDFF, and yield, when compared to plants that received no N in August. This suggests that fertilizing with N in August of the off-year could benefit the blackberry plant.

In 1997, when 'Marion' on-year plants were fertilized in March, May, or March/May, the split application led to a higher mean dry weight, and N and NDFF content, with a trend toward allocating more dry weight, N, and NDFF to the floricanes, and less to the primocanes and primocane leaves. In 1997, a split March/May application also produced a higher mean yield, fruit weight, and total fruit N than a single March or May application. However, the single May application led to the highest mean percent and total fruit NDFF. In 1998, on-year plants treated with a single May application tended to have the highest mean %N and N content and NDFF, but there were no consistent differences in yield between single or split applications. When N was applied closer to fruiting, more N was found in the fruit, but this was not correlated with yield. These results suggest that either a split application in March/May or a single application in May would be better than a single application in March in on-year plants. On-year plants treated with N in both

the off- and on-years in March/Aug or May had the highest mean total dry weight, N, and those treated in August the lowest. August and March/May/August applications produced the highest mean fruit yield and the March/Aug the lowest.

In 1998, off-year 'Marion' plants that received fertilizer in both years had significantly more dry weight (3.4 times as much) and N content (5 times as much) than those that received N in only the on-year of 1997. Plants that received N in only the on-year allocated more dry weight and N to the crowns and less to the primocane leaves than plants that received N in both years. In 1998, on-year plants that received N in both years also had a higher mean plant and fruit yield dry weight and N content than those that received N in only the off-year of 1997.

In plants fertilized in only the off-year (1997) and not the following on-year, the March/August application produced the highest mean yield and N partitioning in fruit in 1998, whereas plants treated only in August contained the highest mean dry weight, N content, and NDFF, and the March/Aug-treated plants the lowest.

Thus, in AY production systems, fertilizing in both years is recommended. A split application of N in March, May, and August produced the best combination of dry weight gain, NDFF, and yield in the potted 'Marion'.

Although this research provided information on 'Marion' and 'Kotata' N partitioning and movement in AY systems, additional studies could add more detail to the current understanding of blackberry N physiology. Root dry weight, N, and NDFF could not be measured in this study, but these values would greatly help determine the N dynamics in the blackberry plant. The use of ^{15}N could further the knowledge of N uptake and partitioning in the EY system compared directly to the AY system; does the plant move or store N differently when grown in the EY or AY system?

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APPENDIX

Table A-1. 1997 and 1998 year-effect on dry weight, N concentration and N content in 'Kotata' blackberries. P-values from t-tests, each date compared separately.

Tissue		Apr	Jun	Jul	Aug	Oct
Dry weight (g)						
Off-year	Crowns	0.492	0.238	0.528	0.190	0.299
Off-year	Primocanes	0.754	0.219	0.597	0.003	0.014
Off-year	P. leaves	0.098	0.498	0.022	0.002	0.596
	<i>Off-year Total</i>	<i>0.512</i>	<i>0.533</i>	<i>0.136</i>	<i>0.060</i>	<i>0.567</i>
On-year	Crowns	0.060	0.008	0.018	0.201	0.004
On-year	Primocanes	0.115	0.115	0.283	0.294	0.075
On-year	P. leaves	0.000	0.046	0.248	0.493	0.361
On-year	Floricanes	0.005	0.286	0.006	0.000	0.053
On-year	Laterals	0.104	0.037	0.286	0.002	0.013
On-year	Unripe fruit		0.065	0.031		
On-year	Ripe fruit			0.437		
	<i>On-year total</i>	<i>0.009</i>	<i>0.531</i>	<i>0.068</i>	<i>0.866</i>	<i>0.003</i>
N conc. (%)						
Off-year	Roots	0.005	0.094	0.460	0.028	0.953
Off-year	Crowns	0.020	0.031	0.000	0.011	0.017
Off-year	Primocanes	0.675	0.122	0.523	0.200	0.003
Off-year	P. leaves	0.020	0.000	0.181	0.133	0.427
On-year	Roots	0.077	0.422	0.287	0.772	0.931
On-year	Crowns	0.112	0.180	0.143	0.669	0.420
On-year	Primocanes	0.166	0.481	0.787	0.035	0.687
On-year	P. leaves	0.001	0.771	0.317	0.361	0.147
On-year	Floricanes	0.068	0.902	0.038	0.424	0.004
On-year	Laterals	0.132	0.787	0.224	0.490	0.466
On-year	Unripe fruit		0.466	0.658		
On-year	Ripe fruit			0.024		
N content (g)						
Off-year	Crowns	0.081	0.012	0.069	0.011	0.027
Off-year	Primocanes	0.698	0.067	0.728	0.019	0.031
Off-year	P. leaves	0.359	0.914	0.014	0.005	0.481
	<i>Off-year Total</i>	<i>0.089</i>	<i>0.293</i>	<i>0.061</i>	<i>0.021</i>	<i>0.915</i>
On-year	Crowns	0.024	0.022	0.036	0.350	0.028
On-year	Primocane	0.140	0.185	0.175	0.011	0.139
On-year	P. leaves	0.001	0.021	0.230	0.409	0.477
On-year	Floricanes	0.007	0.305	0.006	0.007	0.004
On-year	Laterals	0.149	0.086	0.449	0.015	0.012
On-year	Unripe fruit		0.032	0.045		
On-year	Ripe fruit			0.563		
	<i>On-year total</i>	<i>0.038</i>	<i>0.778</i>	<i>0.382</i>	<i>0.041</i>	<i>0.004</i>

Table A-2. Linear regression equations for dry weight partitioning over time in on- and off-year 'Kotata' blackberry, 1997-98.

Tissue component	Equation ^z	r ²	P-value
<i>1997 – off-year</i>			
Crown	y = 2.1 x + 505.7	0.36	0.005
Primocane	y = 11.9 x – 1432.1	0.96	0.000
Primocane leaves	y = 5.1 x – 344.8	0.60	0.000
Total	y = 19.0 x – 1271.2	0.91	0.000
<i>1997 – on-year</i>			
Crown	y = 0.5 x + 737.3	0.05	0.363
Primocane	y = 2.1 x – 161.0	0.45	0.001
Primocane leaves	y = 1.0 x – 13.0	0.23	0.031
Floricanes	y = 1.0 x + 1192.7	0.05	0.350
Lateral	y = - 1.2 x + 1022.5	0.04	0.431
Total	y = 3.4 x + 2778.4	0.16	0.085
<i>1998 – off-year</i>			
Crown	y = 2.2 x + 577.6	0.32	0.012
Primocane	y = 17.6 x – 2380.0	0.27	0.024
Primocane leaves	y = 3.7 x – 225.8	0.57	0.000
Total	y = 23.5 x – 2028.2	0.36	0.006
<i>1998 – on-year</i>			
Crown	y = 3.3 x + 590.4	0.35	0.006
Primocane	y = 3.8 x – 327.6	0.11	0.157
Primocane leaves	y = 1.0 x – 124.4	0.62	0.000
Floricanes	y = 0.7 x + 1804.8	0.02	0.525
Laterals	y = 0.2 x + 604.7	0.01	0.708
Total	y = 9.4 x + 2547.9	0.32	0.009

^z y- dry weight of component indicated (kg/plant); x = day (January 1 = day 1)

Table A-3. Mean dry weight per plant (n=4). Comparison of tissues for 'Kotata' in 1997 and 1998. Total plant dry weight in *Italics*.

Tissue ^z		Apr	Jun	Jul	Aug	Oct
1997						
Off	Crown	755.6 a ^y	761.5 a	1010.1 a	940.6 a	1091.3 a
Off	Primocanes	9.4 b	459.4 b	838.7 a	1192.7 b	2056.3 b
Off	P. leaves	15.9 b	459.9 b	896.7 a	1019.9 a	834.5 a
	<i>Total</i>	<i>780.8</i>	<i>1680.8</i>	<i>2745.5</i>	<i>3153.2</i>	<i>3982.0</i>
On	Crown	853.6 a	689.6 a	846.8 a	908.5 a	867.5 a
On	Primocane	7.5 b	173.5 b	306.8 b	433.1 b	338.8 b
On	P. leaves	3.7 b	197.8 b	243.7 b	305.9 b	178.3 b
On	Floricanes	1349.8 c	1371.4 c	1464.8 c	1168.7 c	1600.3 c
On	Laterals	579.8 d	1113.2 d	619.8 d	1272.3 c	351.3 b
On	Unripe Fruit	NA	676.3 a	542.8 d	NA	NA
On	Fruit	NA	NA	271.0 b	NA	NA
	<i>Total</i>	<i>2794.2</i>	<i>4221.7</i>	<i>4295.8</i>	<i>4088.4</i>	<i>3336.0</i>
1998						
Off	Crown	889.3 a	788.2 a	927.0 a	1081.0 a	1282.1 a
Off	Primocanes	10.5 b	387.3 b	770.0 a	690.0 b	1126.8 a
Off	P. leaves	10.4 b	560.0 b	652.0 b	568.3 b	729.3 b
	<i>Total</i>	<i>910.1</i>	<i>1735.5</i>	<i>2349.4</i>	<i>2339.8</i>	<i>3138.1</i>
On	Crown	1107.5 a	1081.2 a	1175.0 a	1031.0 a	1773.6 a
On	Primocane	4.3 b	104.5 b	202.8 b	339.0 b	684.0 b
On	P. leaves	0.7 b	90.3 c	184.3 b	253.5 b	233.5 c
On	Floricanes	2003.8 c	1753.3 d	2034.0 c	1834.0 c	2124.5 a
On	Laterals	461.8 d	815.5 a	771.3 d	663.5 d	556.8 bc
On	Unripe Fruit	NA	879.5 a	249.5 b	NA	NA
On	Fruit	NA	NA	279.3 b	NA	NA
	<i>Total</i>	<i>3578.5</i>	<i>4724.3</i>	<i>4914.2</i>	<i>414.6</i>	<i>5375.5</i>

^zOn = plants grown in the on-year (fruiting); off = plants grown in the off-year (vegetative); P. Leaves = primocane leaves.

^yMeans in the same column followed by the same letter are not significantly different (Anova, Fisher's LSD, P<0.05)

Table A-4. Comparison of means of on-year and off-year tissue dry weight in 'Kotata' in 1997 and 1998 (n=4). Anova, Fishers LSD, $P < 0.05$.

Tissue ^z		April	June	July	August	October
1997						
Off	Crown	755.6 a ^x	761.5 a	1010.1 a	940.6 a	1091.3 a
On	Crown	853.6 a	689.6 a	846.8 a	908.5 a	867.5 b
Off	Primocanes	9.4 a	459.4 a	838.7 a	1192.7 a	2056.3 a
On	Primocanes	7.5 a	173.5 a	306.8 b	433.1 b	338.8 b
Off	P. Leaves	15.9 a	459.9 a	896.7 a	1019.9 a	834.5 a
On	P. Leaves	3.7 a	197.8 a	243.7 b	305.9 b	178.3 b
Off	Total	780.8 a	1680.8 a	2745.5 a	3153.2 a	3982.0 a
On ^y	Total	2794.2 b	4221.7 b	4295.8 b	4088.4 b	3336.0 a
1998						
Off	Crown	889.3 a	788.2 a	927.0 a	1081.0 a	1282.1 a
On	Crown	1107.5 b	1081.2 a	1175.0 b	1031.0 a	1773.6 b
Off	Primocanes	10.5 a	387.3 a	770.0 a	690.0 a	1126.8 a
On	Primocanes	4.8 b	104.5 a	202.8 b	339.0 b	684.5 b
Off	P. Leaves	10.4 a	560.0 a	652.0 a	568.3 a	729.3 a
On	P. Leaves	0.7 b	90.3 b	184.3 b	253.5 b	233.5 b
Off	Total	910.1 a	1735.5 a	2350.4 a	2339.8 a	3138.1 a
On ^y	Total	3578.5 b	4724.1 b	4913.5 b	4121.6 b	5375.5 b

^zOn = plants grown in the on-year (fruiting); off = plants grown in the off-year (vegetative); P. Leaves = primocane leaves.

^y On-year total includes floricanes, laterals, and fruit.

^xMeans in the same column within tissue type followed by the same letter are not significantly different (Anova, Fisher's LSD, $P < 0.05$)

Table A-5. Linear regression equations for nitrogen concentration over time in on- and off-year 'Kotata' blackberry, 1997-98.

Tissue component	Equation ²	r ²	P-value
<i>1997 – off-year</i>			
Roots	$y = -0.002x + 1.537$	0.525	0.000
Crowns	$y = -0.000x + 0.600$	0.005	0.757
Primocanes	$y = -0.013x + 4.106$	0.773	0.000
Primocane leaves	$y = -0.008x + 3.927$	0.775	0.000
<i>1997 – on-year</i>			
Roots	$y = -0.002x + 1.513$	0.259	0.022
Crowns	$y = -0.000x + 0.691$	0.031	0.460
Primocanes	$y = -0.010x + 3.353$	0.542	0.000
Primocane leaves	$y = -0.009x + 4.239$	0.874	0.000
Floricanes	$y = -0.002x + 1.080$	0.606	0.000
Laterals	$y = -0.012x + 4.230$	0.965	0.000
<i>1998 – off-year</i>			
Roots	$y = -0.003x + 2.035$	0.360	0.007
Crowns	$y = -0.000x + 0.829$	0.014	0.628
Primocanes	$y = -0.012x + 3.737$	0.783	0.000
Primocane leaves	$y = -0.010x + 4.327$	0.826	0.000
<i>1998 – on-year</i>			
Roots	$y = -0.003x + 1.956$	0.372	0.004
Crowns	$y = -0.001x + 0.808$	0.210	0.042
Primocanes	$y = -0.011x + 3.701$	0.770	0.000
Primocane leaves	$y = -0.014x + 5.408$	0.812	0.000
Floricanes	$y = -0.002x + 1.176$	0.550	0.000
Laterals	$y = -0.012x + 4.317$	0.958	0.000

²y – concentration of N of component indicated (kg/plant); x = day (January 1=day1)

Table A-6. Mean nitrogen concentration (n=4). Comparison of tissues for 'Kotata' in 1997 and 1998.

		Tissue ^z	Apr	Jun	Jul	Aug	Oct
1997	Off	Roots	1.26 a ^y	1.29 a	1.09 a	1.03 a	0.94 a
	Off	Crown	0.67 b	0.55 b	0.50 b	0.52 b	0.65 b
	Off	Primocanes	3.06 c	1.67 c	1.05 a	0.87 a	0.70 b
	Off	P. leaves	3.03 c	2.90 d	2.26 c	2.06 c	1.83 c
	On	Roots	1.39 a	1.25 a	1.06 a	1.07 a	1.11 a
	On	Crown	0.69 b	0.63 b	0.65 b	0.63 b	0.72 b
	On	Primocane	2.93 c	1.16 a	0.99 c	1.24 c	0.95 ac
	On	P. leaves	3.36 d	2.81 c	2.29 a	2.05 d	1.85 d
	On	Floricanes	0.85 b	0.74 b	0.64 b	0.74 b	0.47 e
	On	Laterals	2.89 c	2.21 d	2.02 d	1.62 e	0.80 bc
	On	Unripe Fruit		2.84 c	3.11 e		
	On	Ripe Fruit			1.70 f		
1998	Off	Roots	1.65 a	1.49 a	1.18 a	1.67 ab	0.95 a
	Off	Crown	0.86 b	0.77 b	0.75 b	0.76 a	0.83 a
	Off	Primocanes	2.96 c	1.44 a	1.12 a	0.99 a	0.78 a
	Off	P. leaves	3.58 d	2.53 c	2.04 c	2.30 b	1.73 b
	On	Roots	1.77 a	1.15 a	1.25 a	1.02 ac	1.12 a
	On	Crown	0.80 b	0.65 b	0.59 b	0.62 c	0.67 b
	On	Primocane	3.13 c	1.25 a	0.96 c	0.95 ac	0.91 c
	On	P. leaves	4.39 d	2.77 c	2.18 d	1.98 b	1.74 d
	On	Floricanes	1.05 b	0.74 b	0.78 bc	0.69 c	0.68 b
	On	Laterals	3.07 c	2.24 d	1.89 e	1.54 ab	0.89 c
	On	Unripe Fruit		2.91 c	2.35 d		
	On	Ripe Fruit			1.42 a		

^zOn = plants grown in the on-year (fruiting); off = plants grown in the off-year (vegetative); P. Leaves = primocane leave

^yMeans in the same column followed by the same letter are not significantly different (Anova, Fisher's LSD, P<0.05)

Table A-7. Linear regression equations for N content over time in on- and off-year 'Kotata' blackberry, 1997-98.

Tissue component	Equation ^z	r ²	P-value
<i>1997 – off-year</i>			
Crown	y = 0.013 x + 2.63	0.35	0.006
Primocane	y = 0.077 x – 6.71	0.84	0.000
Primocane leaves	y = 0.086 x – 2.81	0.41	0.003
Total	y = 0.176 x – 6.88	0.68	0.000
<i>1997 – on-year</i>			
Crown	y = 0.005 x + 4.58	0.07	0.273
Primocane	y = 0.020 x – 1.26	0.41	0.002
Primocane leaves	y = 0.016 x + 1.05	0.12	0.134
Floricanes	y = - 0.024 x + 14.13	0.38	0.004
Lateral	y = - 0.084 x + 31.93	0.35	0.006
Total	y = - 0.067 x + 50.43	0.16	0.077
<i>1998 – off-year</i>			
Crown	y = 0.016 x + 4.84	0.24	0.032
Primocane	y = 0.044 x – 2.77	0.60	0.000
Primocane leaves	y = 0.061 x – 1.50	0.40	0.004
Total	y = 0.120 x + 0.57	0.60	0.000
<i>1998 – on-year</i>			
Crown	y = 0.015 x + 5.34	0.11	0.159
Primocane	y = 0.034 x – 4.17	0.63	0.000
Primocane leaves	y = 0.024 x – 1.57	0.45	0.001
Floricanes	y = - 0.034 x + 22.24	0.25	0.027
Laterals	y = 0.058 x + 23.84	0.46	0.001
Total	y = - 0.019 x + 45.67	0.03	0.439

^zy - N content of component indicated (kg/plant); x = day (January 1 = day 1)

Table A-8. Mean N content (n=4). Comparison of tissues for 'Kotata' in 1997 and 1998

		Tissue ^z	Apr	Jun	Jul	Aug	Oct
1997	Off	Crown	4.9 a ^y	4.2 a	5.0 a	4.9 a	7.1 a
	Off	Primocanes	0.3 b	7.7 b	8.9 a	10.4 b	14.4 b
	Off	P. leaves	0.5 b	13.4 c	20.2 b	21.1 c	15.5 b
		<i>Total</i>	5.7	25.3	34.1	36.4	37.0
	On	Crown	5.9 a	4.4 ab	5.5 bc	5.7 a	6.2 ac
	On	Primocane	0.2 b	2.0 a	2.9 c	5.3 a	3.2 ab
	On	P. leaves	0.1 b	5.4 b	5.6 bc	6.3 a	3.3 ab
	On	Floricanes	11.5 c	10.1 c	9.4 ab	8.6 a	7.4 c
	On	Laterals	16.7 d	24.7 d	12.5 a	21.0 b	2.8 b
	On	Unripe Fruit		19.1 e	17.6 d		
	On	Ripe Fruit			4.6 c		
		<i>Total</i>	34.4	65.7	58.1	46.9	22.9
1998	Off	Crown	7.6 a	6.8 a	6.9 a	8.2 a	10.5 a
	Off	Primocanes	0.3 b	5.3 a	8.4 a	6.7 a	8.6 a
	Off	P. leaves	0.4 b	13.1 b	13.3 b	12.9 b	12.6 a
		<i>Total</i>	8.33	25.3	28.7	27.8	31.8
	On	Crown	8.9 a	7.0 a	6.9 a	6.3 a	12.0 a
	On	Primocane	0.1 b	1.3 b	1.9 b	3.1 b	6.5 b
	On	P. leaves	0.0 b	2.5 b	4.1 be	5.0 ab	4.0 b
	On	Floricanes	21.2 c	13.1 c	16.0 c	12.6 c	14.4 a
	On	Laterals	14.1 d	18.3 d	14.4 c	10.3 c	4.9 b
	On	Unripe Fruit		25.5 e	5.9 ae		
	On	Ripe Fruit			4.2 e		
		<i>Total</i>	44.4	67.7	53.5	37.4	41.8

^zOn = plants grown in the on-year (fruiting); off = plants grown in the off-year (vegetative); P. Leaves = primocane leave

^yMeans in the same column followed by the same letter are not significantly different (Anova, Fisher's LSD, P<0.05)

Table A-9. Linear regression equations for concentration of nitrogen derived from the fertilizer (NDFF) over time in 'Kotata' blackberry, 1997-98.

Tissue component	Equation ²	r ²	P-value
<i>1997 – off-year</i>			
Roots	$y = 0.106 x - 2.23$	0.617	0.000
Crown	$y = 0.036 x + 1.63$	0.508	0.001
Primocane	$y = 0.059 x + 19.77$	0.265	0.024
Primocane leaves	$y = 0.086 x + 15.72$	0.408	0.003
<i>1997 – on-year</i>			
Roots	$y = 0.157 x - 10.07$	0.833	0.000
Crown	$y = 0.041 x + 1.80$	0.530	0.000
Primocane	$y = 0.112 x + 13.65$	0.265	0.020
Primocane leaves	$y = 0.148 x + 5.76$	0.501	0.000
Floricanes	$y = 0.055 x - 3.37$	0.313	0.010
Laterals	$y = 0.081 x + 2.09$	0.331	0.008
<i>1998 – off-year</i>			
Roots	$y = -0.078 x + 38.72$	0.419	0.003
Crown	$y = -0.020 x + 14.04$	0.153	0.121
Primocane	$y = -0.067 x + 26.97$	0.478	0.001
Primocane leaves	$y = -0.080 x + 30.52$	0.485	0.001
<i>1998 – on-year</i>			
Roots	$y = -0.057 x + 36.93$	0.347	0.006
Crown	$y = -0.020 x + 14.04$	0.135	0.121
Primocane	$y = -0.066 x + 31.87$	0.471	0.001
Primocane leaves	$y = -0.047 x + 24.56$	0.412	0.002
Floricanes	$y = 0.011 x + 31.06$	0.015	0.606
Laterals	$y = -0.510 x + 34.29$	0.211	0.042

²y - dry weight of component indicated (kg/plant); x = day (January 1 = day 1)

Table A-10. Mean concentration of nitrogen derived from the fertilizer (NDFF)(n=4). Comparison of tissues for 'Kotata' in 1997 and 1998.

		Tissue ^z	Apr	Jun	Jul	Aug	Oct
1997	Off	Roots	6.7 a ^y	18.0 ac	18.7 a	23.7 a	24.9 a
	Off	Crown	7.4 a	5.9 b	7.2 b	10.2 b	13.0 b
	Off	Primocanes	25.6 b	28.3 c	30.5 c	38.2 c	32.9 ab
	Off	P. leaves	25.4 b	27.0 c	33.2 c	39.9 c	37.0 c
	On	Roots	9.5 a	14.9 a	17.6 a	26.0 a	36.0 a
	On	Crown	7.8 ad	6.6 b	7.0 b	13.8 b	13.4 bc
	On	Primocanes	18.4 b	38.8 c	38.3 c	42.6 c	40.0 a
	On	P. leaves	15.7 b	32.9 ce	43.7 d	38.9 c	43.1 a
	On	Floricanes	2.8 c	3.9 b	6.2 b	13.7 b	10.2 c
	On	Laterals	5.3 dc	19.5 de	23.1 ae	21.2 ab	21.2 b
	On	Unripe Fruit		28.0 e	28.4 e		
	On	Ripe Fruit			29.3 e		
1998	Off	Roots	27.8 a	28.8 a	23.3 a	19.2 a	14.8 a
	Off	Crowns	13.0 b	11.5 b	7.8 b	7.0 b	10.2 a
	Off	Primocanes	23.4 a	12.7 b	10.9 b	10.7 b	10.3 a
	Off	P. leaves	25.6 a	12.9 b	13.8 b	10.5 b	10.0 a
	On	Roots	31.8 a	22.7 a	29.5 ae	24.4 a	19.7 a
	On	Crowns	15.3 b	14.6 bc	8.7 b	12.5 b	13.0 b
	On	Primocanes	26.6 ac	18.2 ac	17.4 cd	18.9 ac	13.2 b
	On	P. leaves	21.8 cb	15.4 c	13.8 bc	11.6 b	13.6 ab
	On	Floricanes	35.2 a	30.0 d	32.4 a	31.7 d	36.9 c
	On	Laterals	33.9 a	22.6 a	21.9 de	18.1 c	25.1 a
	On	Unripe Fruit		20.0 c	25.3 ef		
	On	Ripe Fruit			19.1 cdf		

^zOn = plants grown in the on-year (fruiting); off = plants grown in the off-year (vegetative); P. Leaves = primocane leave

^yMeans in the same column followed by the same letter are not significantly different (Anova, Fisher's LSD, P<0.05)

Table A-11. Linear regression equations for accumulation of nitrogen derived from the fertilizer (NDFF) over time in 'Kotata' blackberry, 1997-98.

Tissue component	Equation ^z	R ²	P-value
<i>1997 – off-year</i>			
Crown	$y = 0.004 x - 0.24$	0.60	0.000
Primocane	$y = 0.030 x - 3.03$	0.88	0.000
Primocane leaves	$y = 0.042 x - 3.15$	0.54	0.000
Total	$y = 0.019 x + 2.93$	0.10	0.184
<i>1997 – on-year</i>			
Crown	$y = 0.003 x - 0.03$	0.47	0.001
Primocane	$y = 0.009 x - 0.63$	0.42	0.002
Primocane leaves	$y = 0.007 x + 0.18$	0.16	0.078
Floricanes	$y = 0.004 x - 0.08$	0.18	0.060
Lateral	$y = -0.004 x + 3.50$	0.01	0.004
Total	$y = -0.067 x + 50.43$	0.16	0.077
<i>1998 – off-year</i>			
Crown	$y = 0.000 x + 0.77$	0.00	0.861
Primocane	$y = 0.005 x - 0.26$	0.32	0.012
Primocane leaves	$y = 0.005 x + 0.26$	0.13	0.127
Total	$y = 0.010 x + 0.77$	0.22	0.041
<i>1998 – on-year</i>			
Crown	$y = 0.000 x + 1.01$	0.00	0.861
Primocane	$y = 0.005 x - 0.50$	0.66	0.000
Primocane leaves	$y = 0.003 x - 0.19$	0.38	0.004
Floricanes	$y = -0.010 x + 7.01$	0.12	0.127
Laterals	$y = -0.022 x + 7.41$	0.79	0.000
Total	$y = -0.024 x + 14.71$	0.38	0.004

^zy - dry weight of component indicated (kg/plant); x = day (January 1 = day 1)

Table A-12. Accumulation of nitrogen derived from the fertilizer (NDFF) in tissues (g)² (n=4). Comparison of tissues for 'Kotata' in 1997 and 1998.

		Tissue ²	Apr	Jun	Jul	Aug	Oct
1997	Off	Crowns	0.36 a ^y	0.24 a	0.35 a	0.50 a	1.00 a
	Off	Primocanes	0.07 b	2.13 b	2.61 b	4.01 b	5.14 b
	Off	P. leaves	0.12 b	3.36 c	6.77 c	8.43 c	6.27 b
		<i>Total</i>	<i>0.55</i>	<i>6.00</i>	<i>9.74</i>	<i>12.95</i>	<i>12.41</i>
	On	Crowns	0.45 a	0.29 a	0.38 a	0.80 a	0.84 a
	On	Primocanes	0.04 b	0.72 ab	1.02 ab	2.21 a	1.26 a
	On	P. leaves	0.02 cb	1.84 b	2.44 bc	2.33 a	1.39 a
	On	Floricanes	0.32 a	0.41 a	0.61 ac	1.21 a	0.81 a
	On	Laterals	0.88 d	4.85 cd	2.80 b	4.60 b	0.57 a
	On	Unripe Fruit		5.13 d	5.25 d		
	On	Ripe Fruit			0.89 ab		
		<i>Total</i>	<i>1.71</i>	<i>13.24</i>	<i>13.40</i>	<i>11.15</i>	<i>4.87</i>
1998	Off	Crowns	1.02 a	0.79 ab	0.55 a	0.59 a	1.09 a
	Off	Primocanes	0.07 b	0.67 a	0.91 a	0.76 a	0.98 a
	Off	P. leaves	0.10 b	1.69 b	1.85 b	1.39 a	1.28 a
		<i>Total</i>	<i>1.19</i>	<i>3.15</i>	<i>3.31</i>	<i>2.75</i>	<i>3.35</i>
	On	Crowns	1.38 a	1.05 a	0.59 a	0.79 a	1.09 a
	On	Primocanes	0.04 b	0.24 a	0.33 a	0.59 a	0.81 ac
	On	P. leaves	0.01 b	0.37 a	0.58 a	0.57 a	0.56 ad
	On	Floricanes	7.34 c	3.95 b	5.11 b	4.05 b	5.26 b
	On	Laterals	4.79 d	4.05 b	3.19 c	1.82 c	1.20 cd
	On	Unripe Fruit		5.11 c	1.39 d		
	On	Ripe Fruit			0.80 ad		
		<i>Total</i>	<i>13.56</i>	<i>14.77</i>	<i>12.00</i>	<i>7.61</i>	<i>7.86</i>

²On = plants grown in the on-year (fruiting); off = plants grown in the off-year (vegetative); P. Leaves = primocane leave

^yMeans in the same column followed by the same letter are not significantly different (Anova, Fisher's LSD, P<0.05)