



# **Rôle des nutriments dans l'enracinement et le rendement en fruits chez la chicouté (*Rubus chamaemorus*)**

**Mémoire**

**Jade Boulanger Pelletier**

**Maîtrise en biologie**  
Maître ès sciences (M.Sc.)

Québec, Canada

© Jade Boulanger Pelletier, 2016

# **Rôle des nutriments dans l'enracinement et le rendement en fruits de la chicouté (*Rubus chamaemorus*)**

**Mémoire**

**Jade Boulanger Pelletier**

Sous la direction de :

Line Lapointe, directrice de recherche

## Résumé

La chicouté (*Rubus chamaemorus* L.) pousse naturellement dans les tourbières ombrotrophes. La culture de la chicouté dans les tourbières en fin d'exploitation serait très intéressante afin de maintenir des activités économiques sur ces sites ainsi que d'améliorer la disponibilité de ce petit fruit pour une future commercialisation. L'implantation de cette culture fait toutefois face à certains problèmes tels la faible survie des boutures au cours de la première année et un rendement fruitier très variable.

Des essais de fertilisation et d'application d'auxine ont été réalisés pour augmenter la production de racines sur les boutures de rhizome au moment de la plantation afin de réduire leur mortalité. La fertilisation a permis d'augmenter la longueur des racines, mais seulement à la fin de la saison. Les fertilisants ont également stimulé la croissance des plants. Par contre, les concentrations d'auxine utilisées ont entraîné une très forte mortalité des boutures de chicouté. Aucun de ces traitements n'a permis d'augmenter la survie des boutures lors de la plantation. Afin de mieux comprendre les limitations nutritives liées aux faibles rendements fruitiers, nous avons utilisé une analyse compositionnelle (CND) nous permettant d'identifier les déséquilibres nutritifs. Cette analyse a montré que les parcelles moins productives sont caractérisées par une concentration foliaire plus élevée en manganèse, fer, soufre et cuivre.

Les résultats de ce projet de maîtrise vont permettre d'améliorer la régulation de fertilisation lors de la plantation de la chicouté en tourbière résiduelle, mais d'autres recherches doivent être menées afin de réduire la mortalité des boutures lors de la plantation.

## Abstract

Cloudberry (*Rubus chamaemorus* L.) grows naturally in ombrotrophic peatlands. Cloudberry cultivation in peatland after peat extraction has ceased could maintain economic activities on these sites and increase fruit availability for future commercialization. However, the establishment of cloudberry cultivation face some problems, such as low survival rate of the transplants during the first year and a very variable fruit yield.

Fertilization and auxin treatments were tested to increase root production on transplants at planting in order to reduce their mortality. Fertilizers increased root length but only at the end of the season. Plant growth was also improved by the fertilization treatments. On the contrary, the application of auxin led to a high mortality of transplants. None of the treatment applied improved transplant survival at planting. In order to better understand the nutritional limitations that cause low yield, we used a compositional nutrient diagnostic (CND) to identify nutrient imbalances. CND analysis indicated that low yield plots are characterized by higher foliar concentrations of manganese, iron, sulfur and copper.

The present results will help improve fertilization of cloudberry when planted in cutover peatland, but more research is needed to reduce transplant mortality at planting.

# Table des matières

Résumé .....	iii
Abstract.....	iv
Table des matières .....	v
Liste des tableaux .....	vii
Liste des Figures .....	viii
Remerciements.....	ix
Avant-propos .....	x
Chapitre 1. Introduction.....	1
1.1 Mise en contexte .....	2
1.2 La biologie de l'espèce.....	4
1.3 Problématiques liées à la transplantation .....	5
1.3.1 Fertilisation.....	6
1.3.2 Auxines .....	7
1.4 Problématiques liées aux rendements fruitiers.....	8
1.4.1 Limitations nutritionnelles.....	8
1.5 Projet.....	10
1.6 Objectifs et hypothèse.....	10
Chapitre 2. Fertilizers stimulate root production in cloudberry ( <i>Rubus chamaemorus</i> ) rhizomes transplanted in a cutover peatland .....	12
2.1 Résumé .....	13
2.2 Abstract .....	14
2.3 Introduction.....	15
2.4 Materials and methods .....	17
2.4.1 Experimental Field Site .....	17
2.4.2 Fertilization Experiment.....	17
2.4.3 Auxin Experiment.....	20
2.5 Results and discussion.....	21
2.5.1 Soil Properties.....	21
2.5.2 Fertilization Experiment.....	21
2.5.3 Auxin Experiment.....	29
2.6 Conclusion.....	30
Chapitre 3. Low fruit yields in cloudberry are not associated with low nutrient absorption but rather to high levels of Mn, Fe, Cu and S.....	32
3.1 Résumé .....	33

3.2 Abstract .....	34
3.3 Introduction.....	35
3.4 Material and methods .....	36
3.4.1 Site description.....	36
3.4.2 Compositional Nutrient Diagnostic .....	36
3.4.3 Bimonthly Nutritional Portrait.....	38
3.4.4 Foliar Analysis.....	39
3.5 Results .....	39
3.5.1 Compositional Nutrient Diagnostic .....	39
3.5.2 Bimonthly Nutritional Portrait.....	41
3.6 Discussion .....	45
3.7 Conclusion.....	49
Chapitre 4. Conclusion générale.....	50
Références .....	54
Annexes.....	61
Annexe 1 .....	61
Annexe 2 .....	62
Annexe 3 .....	63

## Liste des tableaux

### Chapitre 2

Table 2.1 Results of ANOVA and a priori contrasts comparing the effects of the different fertilization treatments on plant growth and nutrient concentrations in the first and second growing season for cloudberry transplants of the second trial. ....	22
---	----

### Annexes

Table A1. Caractéristiques de la tourbe selon les traitements de l'expérience fertilisation.....	61
Table A2. Coordonnées GPS de chaque tourbières naturelle utilisée en 2013 et 2014 avec les codes utilisés lors de la saisie de données.....	62
Table A3. Partition binaire séquentielle des balances nutritionnelles utilisées dans l'analyse compositionnelle. ....	63

# Liste des Figures

## Chapitre 2

Figure 2.1 Impact of different fertilization treatments on cloudberry root length (cm) at the final harvest. ....	23
Figure 2.2 Root length (cm) progression in cloudberry during the first growing season for fertilized and control transplants.....	23
Figure 2.3 Impact of mineral fertilization on foliar nutrient concentrations (mg g <sup>-1</sup> ) in cloudberry transplants...	25
Figure 2.4 Impact of mineral fertilization on total leaf area (cm <sup>2</sup> ) produced per rhizome transplant during their first and second growing season.....	26
Figure 2.5 Correlations between total leaf area per rhizome transplant (cm <sup>2</sup> ) and total root length (cm) for the three fertilization treatments to which cloudberry transplants were subjected. ....	27
Figure 2.6 Impact of mineral fertilization on the number of buds and rhizome mass (mg) at the end of the first growing season, and on the number of ramets produced during the second growing season in cloudberry transplants.....	28
Figure 2.7 Impact of auxin treatments (K-IBA) on root length (cm) at the end of the first growing season in cloudberry rhizome transplants. Transplants were either grown in the field or in the greenhouse.....	30

## Chapitre 3

Figure 3.1 Binary classification of cloudberry fruit yield and Mahalanobis distance of the <i>ilr</i> balances for the 31 plots. ....	40
Figure 3.2 Results of Tuckey tests comparing <i>ilrs</i> of TP and TN plots. <i>Ilr</i> difference is significant when its range does not overlap with zero (P<0.05).. ....	40
Figure 3.3 Dendrogram of nutrient balances with boxplot representing the distribution of <i>ilrs</i> among the plots classed as TP or TN. The table contains mean foliar nutrient concentrations in mg g <sup>-1</sup> for TN, TP and FN plots. ....	41
Figure 3.4 Concentrations of 11 nutrients in cloudberry leaves throughout the season of 2013 and 2014. ....	43
Figure 3.5 Total foliar content (mg per leaf) of 11 nutrients in cloudberry leaves throughout the season of 2013 and 2014.....	44

## Conclusion

Figure 4.1 Schéma des résultats de l'expérience de fertilisation des boutures.. ....	51
Figure 4.2 Schéma de la stratégie de relâchement des carboxylates et leurs effets sur la disponibilité des nutriments. ....	52

## Annexes

Figure A 1. Courbe de rétention de l'eau par les échantillons de tourbe par bloc selon les pressions appliquées sur l'échantillon. ....	61
Figure A 2. Carte des tourbières naturelles utilisées pour le chapitre 3. Les points rouges sont les tourbières utilisées en 2013 et les points verts sont les tourbières utilisées en 2014. ....	62



## Remerciements

J'aimerais remercier ma directrice Line Lapointe pour son grand soutien et sa présence constante à l'université, peu d'étudiants gradués ont eu l'occasion de voir leur directrice ou directeur chaque jour durant leur maîtrise. Merci aussi de m'avoir permis de présenter mes résultats en Alberta à l'été 2015.

J'aimerais aussi remercier toute l'équipe du laboratoire Lapointe. Un immense merci à Julie Bussièrès qui m'a guidé au début de ma maîtrise (et qui m'a montré comment faire des tableaux croisés dynamiques, wow ça manquait réellement à mes connaissances!). Je te remercie aussi d'avoir élaboré le dispositif expérimental de l'expérience fertilisation et d'avoir récolté les rhizomes au grand froid avec moi! Merci aussi à Pierre-Paul Dion qui m'a aussi aidé sur le terrain à quelques reprises et à Marie-Pier Denis et Yanwen Dong de m'avoir tenu compagnie dans notre beau bureau sans fenêtre! Je remercie aussi le groupe de recherche en écologie des tourbières (GRET) qui m'ont accueilli dans leur grande famille et en particulier Line Rochefort qui m'a conseillé sur mon projet et mise en contact avec des gens de l'industrie de la tourbe.

Pour ce qui est de mes deux étés au Nouveau-Brunswick je veux remercier l'institut de recherche sur les zones côtières (IRZC) particulièrement Mathieu Quenum, Benoit St-Hilaire, Malick Sall et Marie-Josée Laforge. L'IRZC m'a permis d'utiliser leur laboratoire et leur serre et m'ont offert l'aide d'assistants de terrain. Merci aussi aux gens de la tourbière de la Mousse Acadienne qui ont été très accueillants (on se fait remarquer quand on est la seule fille qui travaille sur la tourbière!). Je les remercie aussi grandement de leur implication financière dans mon projet. Je dois aussi mentionner toute la gang de la maison de Shippagan qui m'a permis de profiter de mes soirées et de me sortir de mon isolement de terrain (c'est tellement agréable d'aller se baigner à la plage après une grosse journée de terrain!).

Ce projet a été conjointement financé par la Mousse Acadienne Ltée, Mitacs accélération, Agriculture et agroalimentaire Canada et le conseil agricole du Nouveau-Brunswick. Merci aussi au CEF pour la bourse offerte afin de présenter à un congrès.

Finalement, je veux remercier tous mes proches (famille et amis) qui se sont intéressés à mon projet de maîtrise et à la chicouté ! Merci à mes parents pour leur support moral et financier. Une merci tout spécial à Nicolas pour son aide répétée sur le terrain et son support durant toute ma maîtrise (tu es le meilleur assistant de terrain, je t'engage n'importe quand!).

Un immense merci!!

## **Avant-propos**

Le chapitre 1 est le résultat d'une revue de littérature sur mon sujet de maîtrise et je l'ai entièrement écrit. Les chapitres 2 et 3 sont sous la forme d'articles scientifiques rédigés en anglais. Un résumé en français est présenté au début de ces deux chapitres. J'ai écrit le mémoire et celui-ci a été entièrement révisé par ma directrice Line Lapointe. Les chapitres 2 et 3 seront soumis pour publication dans des revues scientifiques au cours des prochains mois.

Le dispositif expérimental de fertilisation a été élaboré avec l'aide de Julie Bussières. J'ai travaillé sur l'élaboration des dispositifs expérimentaux pour l'expérience auxine du chapitre 2 et les expériences du chapitre 3. J'ai aussi effectué la récolte de données durant les deux étés de terrain de ma maîtrise. J'ai effectué l'analyse de données avec l'aide de Léon-Étienne Parent et Serge-Étienne Parent pour la section du chapitre 3 sur la CND.

# Chapitre 1. Introduction

## 1.1 Mise en contexte

Les tourbières du Nouveau-Brunswick représentent 140 000 ha soit 2% de la superficie du Nouveau-Brunswick (Ministère de l'énergie et des mines, 2010). Le début de l'exploitation des tourbières et de la production industrielle de tourbe remonte à 1942. Le Nouveau-Brunswick extrait présentement plus de 10 millions de ballots de tourbe par année, principalement pour le marché des substrats de croissance, ce qui fait de la province le plus gros producteur de tourbe au Canada (Ministère de l'énergie et des mines, 2015). L'industrie de la tourbe est l'un des principaux leviers économiques pour les régions du Nord et du Nord-est de la province. Les activités de récolte et de traitement de la tourbe représentent 150 millions de dollars pour ces régions (Ministère de l'énergie et des mines, 2010). L'exploitation de la tourbe n'est pas illimitée puisque cette ressource se régénère beaucoup trop lentement pour permettre une exploitation continue sur un même dépôt tourbeux. Depuis 2001, le gouvernement du Nouveau-Brunswick a adopté la Politique provinciale sur l'extraction de la tourbe et des mises à jour de la Politique en 2005 ont mis l'accent sur la restauration des tourbières en fin de vie commerciale. Un des objectifs de la Politique est de s'assurer qu'à la suite de l'exploitation de la tourbière, celle-ci soit restaurée ou aménagée pour une autre vocation qui conserverait la fonction de base du milieu humide (Ministère de l'énergie et des mines, 2010).

La production de petits fruits pourrait permettre de poursuivre des activités économiques sur les tourbières à la suite de l'exploitation (Groupe de recherche en écologie des tourbières, 2009). La culture en tourbière résiduelle doit s'adapter à plusieurs limitations tels un faible pH et de faibles concentrations en nutriments (Andersen et al., 2011). Certains petits fruits comme le bleuets, la canneberge, l'aronia, l'amélanchier et la chicouté sont déjà adaptés à ces conditions particulières étant donné leur présence en tourbière naturelle (Groupe de recherche en écologie des tourbières, 2009). Des recherches sur l'implantation de ces petits fruits en tourbière résiduelle ont d'ailleurs déjà été menées (Groupe de recherche en écologie des tourbières, 2009). Parmi ces cultures, celle de la chicouté est très intéressante, car le rendement en nature est très faible et variable d'une année à l'autre (Ågren, 1988b) et il n'y a aucun producteur au Canada. Ce petit fruit a une forte valeur monétaire et nutritive et il peut être utilisé dans plusieurs produits comme la confiture et l'alcool (Bellemare, 2007, Jaakkola et al., 2012). La chicouté est un fruit très bien commercialisé en Scandinavie, où l'on y trouve plusieurs produits dérivés (Nilsen, 2005). Le fruit est beaucoup moins

connu au Canada malgré la commercialisation de quelques produits tels des liqueurs (ex. La Chicoutai produite par la SAQ), des confitures et vinaigrettes. Toutefois, le fruit est connu et très apprécié dans les régions où pousse la chicouté : Côte-Nord du Québec, péninsule acadienne, Terre-Neuve, Nunavik, etc. Tous les fruits proviennent de la cueillette en nature, car il n'existe pas, à notre connaissance, une culture commerciale établie. Les cueilleurs se font aussi de plus en plus rares, les jeunes étant peu intéressés à cette cueillette qui se fait dans un milieu difficile: accessibilité des sites, présence d'insectes, faible densité de fruits, etc. (Saastamoinen, 1998). Les difficultés associées à la cueillette rendent les récoltes très recherchées par les compagnies qui produisent des produits dérivés de chicouté telles la SAQ et la Maison de la chicoutai. De plus, beaucoup de cueilleurs gardent leur récolte pour leur propre consommation et celles de leurs proches (Karst & Turner, 2011).

Afin de contourner les problèmes liés à l'approvisionnement en nature, une culture de chicouté (*Rubus chamaemorus*) serait une option. Cependant, l'implantation de la chicouté en tourbière résiduelle fait face à deux importantes problématiques : la faible survie des boutures plantées et le faible rendement fruitier. Afin de bien comprendre les problématiques liées à la culture de la chicouté, il sera présenté en introduction une brève présentation de la biologie de l'espèce et un aperçu des deux problématiques avec les pistes de solutions qui seront étudiées dans ce mémoire.

## 1.2 La biologie de l'espèce

La chicouté (*Rubus chamaemorus*), aussi appelée «cloudberry» en anglais et plaquebière en Acadie, est une plante herbacée pérenne faisant partie de la famille des Rosacées (Marie-Victorin et al., 2002) retrouvée principalement dans les tourbières ombrotrophes (Beaulieu et al., 2001). Elle a une répartition circumpolaire et est présente en Sibérie, en Scandinavie, au Canada et en Alaska (Rapp, 2004). Les tourbières ombrotrophes (bogs) sont des milieux humides qui accumulent de la tourbe et qui sont uniquement alimentés en eau par la pluie (Payette & Rochefort, 2001). La matière organique a un pH acide et est caractérisée par des concentrations faibles en nutriments disponibles tels l'azote et le phosphore (Damman, 1986).

La chicouté se reproduit surtout de manière asexuée grâce à son large réseau de rhizomes. Le rhizome d'un clone mesure en moyenne 9,7 mètres et porte 6 ramets dont seulement 2 portent une fleur (Jean & Lapointe, 2001). Les ramets se situent principalement aux extrémités du réseau de rhizomes, c'est-à-dire sur les nouvelles sections de rhizome (Jean & Lapointe, 2001). La chicouté est dioïque et sa pollinisation est effectuée par les insectes. Le fruit résultant est une agrégation de drupéoles (Taylor, 1971). L'espèce étant dioïque, seules les fleurs femelles produisent un fruit et le rapport des sexes est souvent biaisé en faveur des mâles (Ågren et al., 1986). Cette espèce consacre beaucoup plus d'effort à la reproduction asexuée par le biais de la croissance clonale qu'à la reproduction sexuée. Effectivement, 94% de la biomasse est souterraine et seulement 0,05% de la biomasse est allouée à la reproduction sexuée (Dumas & Maillette, 1987).

La chicouté est une des premières plantes à fleurir en tourbière au printemps, mais sa saison de croissance est courte (Beaulieu et al., 2001). La phénologie change dépendamment de la région où croît la chicouté (Beaulieu et al., 2001); la saison de croissance au Nouveau-Brunswick est plus hâtive que celle de la Côte-Nord du Québec. Au Nouveau-Brunswick, l'émergence du bourgeon se produit à la fin mai et la fleur s'ouvre au début juin avant le déroulement des feuilles. Les feuilles sont pleinement déployées vers la fin juin. Les premiers signes de sénescence des feuilles apparaissent à la mi-juillet durant la maturation du fruit. Pourtant, les conditions climatiques nécessaires à la photosynthèse restent bonnes jusqu'au début du mois de septembre. Le fruit est mature à la fin juillet et la sénescence des feuilles est complétée au début septembre.

### 1.3 Problématiques liées à la transplantation

La transplantation en tourbière résiduelle se fait principalement avec des segments de rhizome récoltés sur les bords de canaux de drainage où la chicouté abonde ou dans des milieux naturels (Bellemare et al., 2009a). Les segments de rhizome doivent être d'une longueur minimale de 20 cm afin de procurer suffisamment de réserves pour la croissance de la bouture (Bellemare et al., 2009a). La chicouté produit très peu de racines en milieu naturel et les boutures en sont souvent dépourvues (Jean & Lapointe, 2001). La mortalité des boutures de chicouté est très élevée. Selon les observations de Bellemare (2007), le taux de mortalité peut atteindre 70% bien qu'en général ce taux est de 50%. L'absence de racines sur les boutures pourrait expliquer leur faible survie, car les rhizomes ayant développé des racines en serre avant la transplantation ont de meilleurs taux de survie (85%, Lapointe, données non publiées). Les rhizomes nus doivent produire des racines et des ramets en utilisant seulement les réserves énergétiques présentes dans le fragment de rhizome transplanté. La production d'un système racinaire permet à la plante d'augmenter le volume de sol exploré afin d'acquérir plus d'eau et de nutriments (Raven et al., 2014). Un bon système racinaire peut aussi servir d'ancrage à la plante et ainsi stabiliser le sol. Dans le cas d'une plantation en tourbière résiduelle, cette stabilisation peut limiter les effets négatifs du ruissellement qui peut emporter une partie du sol ainsi que les plants s'y trouvant. Un meilleur enracinement peut également contrer les effets néfastes du soulèvement gélival qui tend à déplacer les rhizomes vers la surface du sol où ils se dessèchent. La forte mortalité des boutures pourrait être réduite par un développement hâtif d'un système racinaire qui permettrait l'acquisition de nutriments et d'eau pour la croissance de la bouture, tout en ancrant plus solidement la bouture dans le sol.

La production d'un système racinaire chez la chicouté passe par la formation de racines adventives puisqu'elles se développent le long du rhizome. Les racines adventives sont celles qui se développent directement sur les tiges aériennes ou souterraines (rhizomes) (Hartmann et al., 2011). La formation de racines adventives peut se résumer en deux principales phases, soit l'initiation et l'élongation de la racine (Hartmann et al., 2011). La formation de racines adventives peut être affectée par plusieurs signaux externes provenant de l'environnement et par des hormones de

croissance (Blazich, 1988b). Les effets de la fertilisation et de l'ajout d'auxine, une hormone de croissance, sur la production de racines seront approfondis au cours de la présente étude.

### 1.3.1 Fertilisation

La fertilisation est amplement utilisée dans l'agriculture moderne afin d'augmenter les rendements des végétaux cultivés. La fertilisation minérale et la production de racines adventives sont reliées, mais les études portant sur l'effet de la fertilisation sur les différentes phases de la production de racines adventives sont peu nombreuses (Blazich, 1988b). L'initiation des racines est principalement stimulée par des hormones de croissance endogènes ou exogènes, mais certains nutriments sont également associés aux processus métaboliques reliés à la formation des racines. Par exemple, la disponibilité du zinc peut influencer la production d'auxines endogènes, le zinc étant nécessaire à la production du tryptophane, un des précurseurs des auxines (Leopold, 1963). La présence du calcium peut influencer le nombre de racines produit par une bouture (Schwambach et al., 2005) puisqu'il est impliqué dans le transport des auxines et la prolifération des cellules (Blazich, 1988b). L'effet de la fertilisation sur l'initiation de racines est surtout déterminé grâce au pourcentage d'enracinement et au nombre de racines, qui sont des mesures secondaires de l'initiation racinaire puisque l'initiation se déroule au niveau cellulaire. Pour la seconde phase de production racinaire, soit l'élongation des racines, l'effet des fertilisants est mieux documenté et a été testé sur plusieurs espèces. Le phosphore et l'azote sont des éléments souvent identifiés comme des stimulants de la croissance racinaire (Marschner, 2012).

La fertilisation minérale au sol augmente la production racinaire chez plusieurs espèces (Fageria & Moreira, 2011), mais la croissance racinaire peut aussi être stimulée par l'absence de nutriments dans le sol. Effectivement, certaines espèces utilisent une stratégie complètement différente qui consiste à augmenter leur production racinaire lorsque la concentration en nutriments immobiles comme le phosphore est faible. La plante misera alors sur l'exploration maximale du sol pour trouver des secteurs avec de plus fortes concentrations en nutriments (Fernandez & Rubio, 2015, Wang et al., 2015). Cette stratégie de production racinaire en réponse à de faibles concentrations de nutriments implique d'investir beaucoup de carbone pour la production de racines (Lynch & Ho, 2005) sans être assuré de trouver des secteurs à fortes concentrations nutritives. La chicouté semble



répondre à la fertilisation en augmentant sa masse racinaire (Gauci, 2008), mais des mesures plus hâtives sont nécessaires pour déterminer si l'induction ou la croissance des racines sont stimulées par une fertilisation minérale.

### 1.3.2 Auxines

Les auxines sont un groupe d'hormone de croissance impliquée dans le phototropisme, la dominance apicale et la production de racines adventives (Hartmann et al., 2011). L'application d'auxines pour le bouturage commercial est très fréquente puisque les auxines stimulent la production de racines adventives sur des tiges ou des feuilles. L'auxine la plus utilisée commercialement est l'acide indole-3-butérique (AIB) (Leopold, 1963).

Les plantes produisant moins de racines en conditions naturelles seraient plus sensibles à l'application d'auxine en raison d'une plus faible concentration d'auxines endogènes (Srivastava, 2002). Le bourgeon apical est la principale source d'auxines endogènes; ces auxines empêchent le développement des bourgeons latéraux (Raven et al., 2014). Lors du bouturage des rhizomes, les fragments sont séparés du bourgeon apical et reçoivent donc moins d'auxines. L'efficacité de l'auxine peut également être affectée par l'âge de la bouture, le temps écoulé entre la récolte et l'application ainsi que par la saison de récolte des boutures. Les boutures récoltées au printemps ou à l'été auraient plus de facilité à s'enraciner que les boutures prélevées à l'automne (Srivastava, 2002). La présence de feuilles sur la bouture peut avoir un impact sur la réussite du bouturage. Les feuilles fournissent une source de carbone pour la formation de racines. Une source de carbohydrates peut soutenir l'initiation et la croissance du nouveau système racinaire (Davis, 1988).

Les boutures peuvent être traitées avec de l'auxine selon plusieurs techniques : application d'une poudre de talc contenant une dose d'auxine, trempage dans une solution diluée d'auxine et trempage rapide dans une solution plus concentrée (Blazich, 1988a). Lors de l'utilisation des solutions, deux formes d'auxine peuvent être utilisées: une auxine sous forme d'acide qui doit être diluée dans l'alcool ou à l'aide d'une base forte et un sel d'auxine (K-IBA), qui peut être dilué dans l'eau (Blazich, 1988a).

## 1.4 Problématiques liées aux rendements fruitiers

La production de fruits chez la chicouté est très variable entre les tourbières, et ce, d'une année à l'autre (Ågren, 1988b). Le rendement peut être affecté négativement par des facteurs environnementaux comme les gels tardifs durant la floraison ou les gels hâtifs durant la maturation des fruits (Ågren, 1988b). Le faible rapport clones femelle/mâle influence aussi le rendement en fruits d'un site. Ce faible rapport peut s'expliquer par une compétitivité moins grande des ramets femelles (Dumas & Maillette, 1987). Effectivement, le coût métabolique peut être plus important chez les plants femelles pour la production d'ovules et de fruits par rapport à la production de pollen et de nectar par les plants mâles (Lloyd, 1974, Korpelainen, 1994, Brown & McNeil, 2009). La production de fruits peut aussi être limitée par les réserves carbonées de la plante (Gauci, 2008). La surface foliaire d'un clone est très faible en comparaison avec la biomasse souterraine de la plante. La plante a donc un fort puits souterrain, en plus des fruits, mais une faible source de carbone. Le succès reproducteur peut aussi être affecté par la disponibilité des nutriments dans le sol; les tourbières ombrotrophes étant des milieux pauvres en nutriments, il est possible que le rendement en fruits soit fortement limité par les nutriments disponibles. D'ailleurs, plusieurs études ont testé l'ajout de fertilisants afin d'augmenter les rendements en fruits de la chicouté. Certaines de ces études ont vu un effet positif sur le rendement quelques années après la fertilisation (Østgård, 1964, Mäkinen & Oikarinen, 1974, Bellemare et al., 2009b), mais l'effet de la fertilisation sur la production de fruits n'est pas concluant dans tous les cas (Taylor, 1971, Kortesharju & Rantala, 1980, Hébert-Gentile et al., 2011) d'où l'intérêt de poursuivre la recherche concernant l'effet des nutriments sur la productivité de la chicouté.

### 1.4.1 Limitations nutritionnelles

Chez les plantes à croissance rapide, les limitations nutritionnelles sont souvent visibles. Effectivement, la plante continue à croître malgré le manque de nutriments, ce qui mène à l'apparition d'une carence minérale importante du feuillage qui se traduit souvent par un symptôme visuel tel une couleur différente ou des taches sur les feuilles (Marschner, 2012). Les plantes à croissance lente, qui sont adaptées aux milieux limités en nutriments, investissent dans la croissance seulement lorsqu'elles ont les nutriments nécessaires (Chapin, 1980). Les symptômes visuels de

carences sont donc absents, mais la croissance et la reproduction sexuée seront limitées (Chapin, 1980).

Une analyse foliaire est nécessaire pour déterminer les nutriments limitant la productivité (Bould, 1968). L'analyse de micronutriments est essentielle chez la chicouté puisque sa croissance semble limitée principalement par un excès de certains métaux plutôt que par une faible abondance des macronutriments (Parent et al., 2013, Bussièrès et al., 2015). Des essais de culture en serre (Bussièrès et al., 2015) et une étude de la nutrition minérale en milieu naturel sur la Côte-Nord (Parent et al., 2013) ont montré que la présence d'aluminium dans la feuille de chicouté était associée à une croissance et à une production de fruits plus faibles. L'aluminium est un élément toxique pour la plante lorsqu'il est présent en trop grande quantité. Cet élément se trouve en faible concentration dans les sols organiques et ne devrait pas être un problème en tourbière, ce qui porte à croire que la chicouté a une faible tolérance à l'aluminium (Parent et al., 2013). L'étude sur les populations de la Côte-Nord montre aussi que le soufre semble être en excès chez les individus moins productifs.

L'utilisation des concentrations en nutriment pour déterminer les déséquilibres nutritionnels peut amener des biais causés par la non-indépendance des nutriments entre eux. Effectivement, les nutriments foliaires sont reliés entre eux et la diminution ou l'augmentation d'un nutriment peut affecter l'absorption des autres nutriments (Parent et al., 2012), en plus de modifier leur concentration, puisqu'il s'agit de pourcentages qui s'additionnent pour atteindre 100% (Parent et al., 2012). Les balances orthogonales de nutriments utilisées dans l'analyse de composition nutritionnelle (CND) par Parent et al. (2012) permet d'éviter les biais d'analyse. Les balances nutritionnelles permettent de déterminer les effets d'un rapport entre nutriments (ex. N/P) sur le rendement de la plante. Le nombre de balances analysées ne peut dépasser le nombre de degrés de liberté associé aux nutriments, par exemple 10 éléments permettent de tester 9 balances et ces balances doivent être orthogonales. Le choix des balances étudiées revient à l'utilisateur qui doit tenir compte des liens connus entre les nutriments ou groupes de nutriments.

Les concentrations foliaires des nutriments sont aussi affectées par les stades phénologiques de la plante et évoluent durant la saison (Marschner, 2012). Chez certaines espèces d'arbustes, les

nutriments mobiles dans les tissus végétaux comme l'azote, le potassium et le phosphore ont tendance à diminuer au cours de la saison, tandis que les nutriments immobiles comme le calcium s'accumulent dans les feuilles au cours de la saison (Grigal et al., 1976). Les changements saisonniers des nutriments sont toutefois différents d'une espèce à l'autre (Guha & Mitchell, 1966, Grigal et al., 1976).

## 1.5 Projet

Ce projet a été effectué en tourbière résiduelle, en tourbière naturelle et en serre. Le projet visait à mieux cibler les fertilisants qui favorisent l'enracinement et fournissent les éléments nutritifs nécessaires à un taux de survie et de développement maximal chez des rhizomes transplantés en tourbière résiduelle. L'effet de l'application d'auxines sur le développement d'un système racinaire a aussi été déterminé en tourbière résiduelle et en serre. De plus, Les changements saisonniers des concentrations en nutriments dans le feuillage de la chicouté ont été suivis en tourbière naturelle afin de déterminer les nutriments qui sont limitants pour la production de fruits.

## 1.6 Objectifs et hypothèse

\*\* Objectif 1: Évaluez l'effet des fertilisants et des auxines sur la survie et la croissance des boutures de chicouté plantées en tourbière résiduelle.

**Hypothèse 1** : La faible disponibilité des nutriments dans les tourbières ombrotrophes limite le développement et la prolifération racinaire.

Prédiction 1 : L'ajout de fertilisants permettra le développement plus hâtif d'un système racinaire qu'en l'absence de fertilisants.

Prédiction 2 : Les boutures fertilisées auront un système racinaire plus long à la fin de la saison de croissance que les boutures non fertilisées.

**Hypothèse 2** : Le développement rapide d'un système racinaire favorise la croissance des boutures.

Prédiction 1 : La croissance mesurée en termes de surface foliaire totale produite par rhizome sera corrélée à la longueur des racines du rhizome puisqu'un système racinaire bien développé permet de puiser les nutriments nécessaires au bon développement des feuilles.

**Hypothèse 3 :** L'absence d'un bourgeon actif, principale source d'auxines endogènes chez la bouture, expliquerait la faible production de racines sur les boutures de chicouté.

Prédiction 1 : Les rhizomes ayant reçu une dose exogène d'auxine auront une plus grande masse racinaire que ceux non traités.

**\*\*Objectif 2 :** Établir le portrait nutritionnel des populations naturelles de chicouté en lien avec la production de fruits

**Hypothèse 3 :** Une partie des nutriments servant au développement et à la maturation du fruit provient des feuilles présentes sur le ramet.

Prédiction 1 : Les concentrations de nutriments dans les feuilles des ramets avec fruits vont diminuer davantage au cours de la saison que dans les feuilles des ramets végétatifs en raison de la translocation d'une partie des nutriments vers le fruit.

**Hypothèse 4 :** En absence de gels lors de la floraison, les faibles rendements fruitiers sont causés par les déséquilibres nutritionnels qui varient en fonction du site.

Prédiction 1 : Les individus se trouvant dans les populations à faible rendement fruitier présentent des déséquilibres nutritionnels au moment de la fructification par rapport aux populations à fort rendement.

Prédiction 2. Les populations de chicouté du Nouveau-Brunswick et de la Côte-Nord vont présenter des déséquilibres nutritionnels différents causés par les différences régionales dans la composition de la tourbe.

**Chapitre 2. Fertilizers stimulate root production in cloudberry (*Rubus chamaemorus*) rhizomes transplanted in a cutover peatland**

## 2.1 Résumé

La chicouté (*Rubus chamaemorus*) est un petit fruit qui pousse naturellement dans les tourbières ombrotrophes. Sa culture dans les tourbières après la fin de l'extraction de tourbe horticole pourrait permettre le maintien d'activités économiques sur ces sites. La chicouté a un bon potentiel de commercialisation au Canada, mais la régie de culture doit être améliorée avant de pouvoir établir des cultures commerciales. Les boutures sont normalement composées de segments de rhizomes récoltés dans les populations naturelles, mais leur faible densité racinaire peut expliquer la faible croissance et les fortes mortalités des boutures durant les premières années de croissance. L'objectif de cette étude était de déterminer l'effet de la fertilisation et de l'application d'auxines sur la production de racines. L'effet de la fertilisation et de l'application d'auxines sur la production de racines ont été testés. Trois doses de fertilisants ont été testées lors de plantation de boutures dépourvues de racines et l'application d'auxine a été testée en serre et sur le terrain. Les récoltes séquentielles de boutures ont permis de quantifier l'évolution de la production de racines durant la saison de croissance. Les systèmes racinaires ont été scannés et analysés avec le programme WinRhizo afin de déterminer la longueur totale des racines.

Les plants fertilisés ont produit des racines deux à quatre fois plus longues après seulement une saison de croissance, mais la fertilisation n'a pas permis d'obtenir un enracinement hâtif. Les boutures produisent des ramets avant d'investir dans la production de racines. L'initiation de la production de racines semble limitée par les réserves carbonées de la plante. Les fertilisants ont stimulé la croissance des plants; ils ont produit de plus grandes feuilles, des rhizomes plus longs et plus de bourgeons à la fin de la saison. L'application d'auxines sur les rhizomes dans les expériences sur le terrain et en serre a mené à de fortes mortalités et n'a pas stimulé la production de racines. Les boutures en serres ont produit six fois plus de racines que les boutures sur le terrain. Nous concluons que la fertilisation peut favoriser l'établissement de la chicouté et sa croissance future ce qui pourrait éventuellement permettre d'augmenter la densité des plants et le rendement fruitier. L'application d'auxines n'est pas recommandée due à la forte mortalité et l'absence d'effet sur la production de racines.

## 2.2 Abstract

Cloudberry (*Rubus chamaemorus*) is a common berry species in ombrotrophic peatlands. Its cultivation in peatlands after horticultural peat extraction has ceased could maintain economic activities on these sites. Cloudberry has good economic potential for Canada, but crop practices must to be improved before commercial production can be established. Rhizome segments that were collected in natural populations are the typical transplant unit, but their very low root density might explain the slow growth and high mortality that is observed during the first few growing seasons. The objective of this study was to determine the effects of mineral fertilization and auxin applications on root growth. The effects of mineral fertilization and auxin applications on root growth were tested. Three NPK fertilizer rates were applied at planting on bare rhizomes in peatland while auxin applications were tested in both greenhouse and field experiments. Sequential harvestings allowed quantifying the progression of root growth during the growing season. Root systems were scanned and analyzed using WinRhizo to determine total root length.

Roots of fertilized plants were two to four times longer than those of control plants after one complete growing season, but fertilization did not lead to early rooting. Rhizome segments produced new ramets before investing in root production. Root initiation appears to be limited by carbohydrate availability. Fertilizers stimulated the overall growth of the transplants; they produced larger leaves, longer rhizomes and a higher number of buds at the end of the season. Auxin applications to the rhizomes incurred high mortality and did not stimulate root production in both field and greenhouse experiments. Transplants grown in greenhouse produced six times more roots and larger leaves than transplants grown in the field. We conclude that fertilizers applied at planting can improve cloudberry establishment and future growth, which could eventually lead to improved plant cover and fruit yield. The application of auxins is not recommended due to the high mortality and the lack of impact on rooting.



## 2.3 Introduction

Cloudberry (*Rubus chamaemorus* L.) is a circumpolar species that grows in ombrotrophic peatlands and produces amber-coloured fruits (Resvoll, 1929). The berries have an established economic value in Scandinavia (Saastamoinen et al., 2000a). In Canada, the fruit is mostly known where it is locally abundant. Commercial cloudberry culture has yet to be developed in both Scandinavia and Canada; all fruits are harvested in natural peatlands. The species is dioecious and the ratio between male and female flowers in natural populations is high; furthermore, fruit abortion is frequent, which constrains fruit yield (Dumas & Maillette, 1987, Ågren, 1988a). The number of pickers has been decreasing in recent years due to the harsh conditions of collecting delicate fruits in natural peatlands. Pickers have declined in number also due to low fruit density, despite a growing demand for and the high economic value of this fruit (Centre d'expertise sur les produits forestiers, 2008). Cultivation in cutover peatlands where peat extraction has ceased could maintain economic activities on these sites, thereby improving plant density and, therefore, fruit yield per hectare.

Cloudberry, a subshrubby plant (Payette, 2015), propagates mainly through its extended system of rhizomes (Taylor, 1971). Rhizome segments that are 20 cm long are commonly used as transplants (Rapp, 2004, Bellemare et al., 2009b). Nevertheless, high mortality of these transplants has been recorded in the field, upwards of 70 % in some years (Bellemare et al., 2009a). Previous studies have indicated that rhizome segments up to 40 cm long do not contain carbon and nutrient reserves that are sufficient to sustain ramet growth that is comparable with of growing shoots attached to an intact rhizome system (Gauci et al., 2009). Furthermore, these rhizome segments are often rootless (Jean & Lapointe, 2001), which most likely limits the uptake of nutrients from the soil. In natural peatlands, cloudberry produces few roots along the rhizome, but these are capable of producing a large root system when grown in containers. Root production in containers, in turn, is strongly influenced by substrate properties. Rhizomes growing in containers for three growing seasons produced 14 times more root biomass and 25 times more total aerial biomass on fibric peat compared to in mesic peat which is more decomposed (Bussi eres et al., 2015). Fibric peat exhibits physical properties that favour the growth of cloudberry (Th eroux-Rancourt et al., 2009), together with higher phosphorus content than mesic peat.

Mineral fertilization stimulates root growth in many species (Fageria & Moreira, 2011). In rootless cuttings, root production must be induced before any root elongation can take place (Hartmann et al.,

2011). The effect of mineral fertilization on the different rooting phases is not very well known (Blazich, 1988c). Fertilization appears mainly to affect the elongation phase of roots without accelerating root initiation (Hartmann et al., 2011), as has been shown in *Petunia*. In the latter case, the application of fertilizers to stem cuttings improves root growth, but only after root emergence has occurred (Santos et al., 2011). Mineral nutrition can increase root length and root number in rootless cuttings of *Eucalyptus globulus* Labill., but rooting time and percent rooting was mostly affected by the application of auxin (Schwambach et al., 2005). In cloudberry, mineral fertilization improved root length after one growing season in a greenhouse experiment, but the timing of root initiation was not determined (Gauci, 2008).

Auxins are commonly used to promote adventitious root production in commercial cuttings (Hartmann et al., 2011). Auxin is a phytohormone that is involved in cell division and known to be an adventitious root formation activator (Pop et al., 2011). Species producing fewer roots are often more sensitive to auxin applications due to their low endogenous auxin concentrations (Srivastava, 2002). Several forms of auxins are used to promote root formation but the most commonly used formulation that is applied to commercial cuttings is indole-3-butyric acid (IBA) (Srivastava, 2002). Auxin addition has been tested in vitro on cloudberry shoot clusters from meristem cultures, where it has been found to promote rooting while inhibiting the formation of new shoots (Martinussen et al., 2004). Thiem (2001) reported on in-vitro and in-vivo auxin application to rootless cloudberry shoots. This study showed that agar-solidified medium containing auxins (IBA and IAA) promoted rooting of the shoots, while shoots did not root in the medium that did not contain auxins. Direct application of powdered IBA to in-vitro shoots prior to being transplanted into peat moss, led to 39 % rooting after eight weeks. Given the absence of a control, the positive effect of auxin applications on in-vivo rooting could not be confirmed (Thiem, 2001). To our knowledge, no studies have reported auxin application trials on rootless rhizome transplants in cloudberry, and very few in other rhizomatous species.

No studies have investigated the phenology of adventitious root production by cloudberry transplants under field conditions. The only known trials on root production in cloudberry transplants are greenhouse experiments (Gauci, 2008, Bussi eres et al., 2015). These rarely reflect what is happening in the field (Mokany & Ash, 2008). The objective of this study was to determine the effect of fertilization and auxin applications on root production and subsequent root growth in cloudberry

rhizome transplants. Sequential harvesting throughout the growing season would allow us to follow root production more closely and determine whether fertilizer and auxin treatments hasten or enhance root production. Earlier rooting might favour transplant survival, whereas enhanced root production during the first growing season may lead to faster rhizome propagation and improved fruit yield after a few years of cultivation.

## **2.4 Materials and methods**

### **2.4.1 Experimental Field Site**

The experimental site is located on Lamèque Island, northeastern New Brunswick (47°48'47"N, 64°37'24"W). This region is characterized by a maritime climate: mild winters and cool humid summers. According to the Bas-Caraquet weather station (47°48'08"N, 64°50'00"W), the mean temperature for the months of May, June, July and August are respectively 9 °C, 14 °C, 19 °C and 19 °C, based on records collected from 1993 to 2007 (Environnement Canada, 2015).

Two experiments were established in a residual section of the peatland that was owned by Acadian Peat Moss (1979) Ltd. (Coteau Road, NB). The drainage ditches that had been used for the peat extraction were still functional and maintaining a low water table during the summer. Rhizomes for the two experiments were collected from the edge of the main drainage ditch on the experimental site and cut into 20 cm segments following the recommendations of Bellemare et al. (2009a). These rhizome segments were of different ages since long rhizomes that have been growing for many years were collected then cut into different segments. Most of the rhizome segments carry at least one visible dormant bud, sometimes more. Given that most rhizome segments are rootless, all roots that remained were cut to standardize among-rhizome segments.

### **2.4.2 Fertilization Experiment**

*Experimental Design:* The fertilization experiment included three blocks and four treatments (three fertilizers and one control), which were randomly assigned randomly within the blocks. The twelve plots each measured 3 m x 9 m, each, and were separated from on another by 2 m each within each block. Two meters separated the first two blocks, while the third block was located on the opposite

side of a small ditch. Each plot contained six rows of 18 rhizomes, for a total of 108 rhizomes per plot. They were planted at a distance of 50 cm from one another.

The three fertilizer treatments differ with regards to N, P and K concentrations: 6 %-12 %-6 %, 6 %-12 %-12 % and 12 %-12 %-12 % (N, P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O). Nitrogen was applied as an equal mixture of ammonium and nitrate. The three fertilizers were applied at rates of 50-100-50 kg ha<sup>-1</sup>, 50-100-100 kg ha<sup>-1</sup> and 100-100-100 kg ha<sup>-1</sup>, respectively. They contained the same amount of the following nutrients: 2.5 % Ca, 1 % Mg, 0.3 % B, 0.3% S, 0.004 % Zn, 0.004 % Cu and 0.004 % Mn. The fertilizer formulations were prepared by Engrais Chaleur (Petit-Rocher, NB).

*First Trial:* Rhizomes were collected in November 2012, returned to the laboratory and maintained in a cold room in damp moss (4° C) until planting in spring 2013. The site was tilled in spring 2013 before plot establishment. Fertilizers were incorporated into the uppermost 6 cm of peat using a rake; control plots were also raked. Rhizomes were then planted at a depth of 5 cm according to Bellemare et al. (2009a).

*Second trial:* A new set of rhizomes were transplanted in 2014 due to transplant survival in spring 2013 (first trial). Rhizomes were collected in October 2013 after leaf senescence was completed and transplanted immediately into the plots. Rhizome transplants remaining from 2013 were replaced with new ones. Following soil analyses in spring 2014, we elected to reapply the same quantity of fertilizer as in 2013, given that nutrient concentrations in the peat did not significantly differ among treatments. The second fertilizer application occurred on June 11. Because of the presence of transplants in the plots, it was impossible to incorporate fertilizers into the peat. Therefore, fertilizers were applied in five trenches (each 5 cm deep) between the rows and covered with peat. We did not broadcast the fertilizers because this would favour growth of competing species (Rapp & Steenberg, 1977). The effect of fertilization on growth was also recorded during the second growing season of the second trial in July 2015 on the remaining rhizomes.

*Plant Measures and Samplings:* The date of emergence and the presence of a ramet were recorded for each transplant in both trials. The number of ramets were recorded again at the beginning of the second growing season (2015) in the second trial. Leaf diagonal (D, cm) was measured and leaf area was then calculated with the following equation;

$$\text{Leaf area (cm}^2\text{)} = 0.5242 \exp^{0.7158 * D}$$

This equation was estimated by measuring D with a ruler, while the corresponding leaf area was determined using a LICOR 3100 area meter (LICOR Biosciences Lincoln, NE) for leaves having a D < 4 cm (Th  roux-Rancourt et al., 2009). The diagonal was measured in 2013 on the transplants in the first trial and in 2014 and 2015 on the transplants in the second trial.

To determine total length of the root system, transplants were dug up carefully to ensure all roots were collected. In 2013, 6 transplants per plot were harvested when possible; only three and five surviving transplants were collected respectively in two of the plots. The low survival from the first trial permitted a single harvest at the end of the summer (6 August). For the second trial, six transplants were collected in each plot on three different dates (10 July, 28 July and 4 October 2014). Each time, the six harvested transplants were selected randomly from the pool of living transplants. The number of ramets and leaves was counted on each harvested rhizome. All underground material was frozen until they could be analyzed using WinRhizo (Regent Instruments Inc., Quebec, QC). This program is an image analysis system designed specifically for roots.

Leaves present on the transplants that were collected in June and July 2014 were subjected to nutrient analysis. Leaves from June and July 2014 were pooled to obtain enough material for nutrient analysis. Leaves were oven-dried at 65   C for 48 hours, then ground with a mortar and pestle. Concentrations of C, N and S were obtained following high-temperature combustion with a LECO CNS-2000 (St-Joseph, MI). The rest of the tissues were digested in perchloric-nitric acid prior to quantifying their nutrient concentrations by plasma emission spectroscopy (ICP-OES) (Barnhisel & Bertshc, 1982).

*Soil Analyses:* Physical and chemical soil analysis were performed in all plots of the fertilization experiment. Three samples were taken from each plot at 0-20 cm depth, then composited. Bulk pH was measured in a 1:10 soil:solution with CaCl<sub>2</sub> (0.01 M). Organic matter content (%) was obtained by combustion at 550   C for 24 h. Nutrient concentrations (P, Al, Fe, Zn, Ca, K, Mg) were determined by inductively coupled plasma- optical emission spectrometry (ICP-OES) after Mehlich-3 extraction (Mehlich, 1984).

Two soil cores were collected in each plot in 2014, using a cylinder (8 cm diameter, 7 cm long); ends of the cores were then covered with nylon mesh. The first set of cores was oven-dried at 105 °C for 48 h and weighed to estimate bulk density ( $D_b$ , g cm<sup>-3</sup>). The remaining cores were used to determine water retention curves using a tension table (Topp & Zebchuk, 1979). Different pressure head were applied (-1, -2, -5 and -10 kPa). Pressure head of -1 and -2 kPa were applied for 24 h, whereas pressure head of -5 and -10 kPa were applied for 48 h. In the latter case, the cores were weighed before applying a new pressure head.

*Statistical Analyses:* All variables from the fertilization experiment were analyzed using one-way ANOVA and a priori contrasts, on mean per block per treatment. We use a priori contrasts to quantify the effect of fertilization (Control vs fertilized treatments), the effect of a fertilizer containing less nitrogen (50-100-100 vs 100-100-100) and the effect of a fertilizer containing less nitrogen and potassium (50-100-50 vs 100-100-100). Two-way ANOVA was performed on root lengths for the samples that had been collected at the end of the season in the first and second trials, using fertilization treatment and trial as fixed factors. Stepwise linear regression with backwards elimination was performed with root length as dependent variable and different growth measurements and foliar nutrients as independent variables. All analyses were performed using Statistix (Statistix 10, Analytical Software, Tallahassee, FL).

### 2.4.3 Auxin Experiment

Auxin trials were performed both in the field and in the greenhouse. Rhizomes were collected in spring 2014 and immediately subjected to one of three treatments: a control and two levels of K-IBA (250 and 500 ppm). The auxin potassium salt was diluted in distilled water prior to use. Ends of the cut rhizomes were dipped for 15 seconds in either the auxin solution or distilled water (control) prior to planting. The main variable that was recorded was root length, which was analyzed on sampled rhizomes using WinRhizo.

*Greenhouse Experiment:* One rhizome was planted per plastic pot (20 x 18 cm). Eight pots per treatment were planned for harvest three times during the season, for a total of 72 pots. Rhizomes were planted on May 21; the first harvest took place after four weeks, the second harvest after seven weeks, and the final harvest occurred after nineteen weeks of growth.

*Field Experiment:* Fifteen plots were established in the same cutover peatland as for the fertilization experiment. The five replicates of the three treatments (0, 250 and 500 ppm K-IBA) were randomly distributed among the 15 plots. Fifty rhizomes were planted in each plot. Sprouting and survival were monitored during the growing season. Transplants were harvested after 19 weeks of growth to measure root length.

## **2.5 Results and discussion**

### **2.5.1 Soil Properties**

Soil physical properties after fertilization application did not differ among the 12 plots. Mean organic matter content was 95.6 % ( $\pm 0.7$  %SE) and bulk density averaged 0.105 g cm<sup>-3</sup> ( $\pm 0.005$  SE). Water retention curves were similar among plots; mean soil porosity ( $\Phi$ ) was 0.96% ( $\pm 0.002$  SE). Soil pH averaged 3.14 ( $\pm 0.006$  SE) among plots (Annexe 1).

### **2.5.2 Fertilization Experiment**

*First Trial:* In the first trial, sprouting was very low, i.e., only 11 %. We attributed this low survival to the fact that rhizomes were planted in the spring rather than in the autumn. Keeping the rhizomes in a cold room throughout the winter appears to incur more damage in some years, although good survival rates were following spring planting in other years (Bellemare et al., 2009a). High mortality prevented us from sampling transplants more than once during the growing season. We did a single harvest after two months of growth, as we were concerned that more transplants would die if we delayed sampling until the end of the season. The effect of fertilization was not significant for either root length ( $F_{3,11} = 3.25$ ,  $P = 0.109$ ) or total leaf area ( $F_{3,11} = 1.83$ ,  $P = 0.213$ ) (Fig. 2.1).

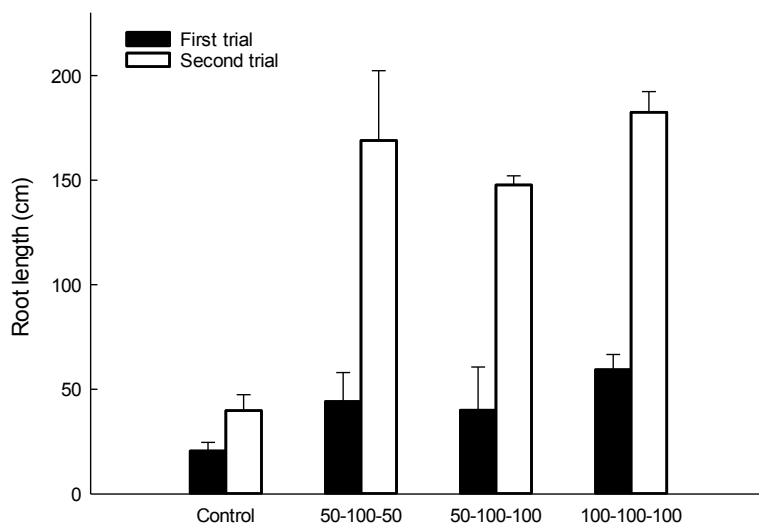
*Second Trial:* Survival averaged 51 % for the second trial. Mineral fertilization increased cloudberry root length, rhizome mass, number of buds, and total leaf area after one growing season, together with the total leaf area and the number of ramets that were produced per transplant during the second growing season (Table 2.1). Roots were produced on the nodes of the existing rhizome. Fertilized plants produced roots that were two to four times longer than those of control plants after one complete growing season (Fig. 2.1). Fertilization treatments did not affect the percentage of sprouting; indeed, it appears that the rhizome should contain carbon and nutrient reserves that are

sufficient to sprout regardless of soil nutrient availability. In terms of NPK, fertilizer composition did not significantly affect root length. When we compared the root length at the final sampling for the two trials (Fig. 2.1), we noted a significant main effects of trial ( $P < 0.001$ ) and fertilization treatment ( $P < 0.001$ ), as well as the trial  $\times$  treatment interaction ( $P = 0.008$ ). The significant interaction indicated that only unfertilized plots exhibited similar root length in the two trials, despite the two additional months of growth during the second trial. Sequential harvests during the second trial showed an important increase in root length in fertilized plots between the second and third harvests (between 8 July and 4 October) (Fig. 2.2). Indeed, the rate of root production in control transplants was constant throughout the season, in contrast with the fertilized transplants, which exhibited a quadratic response (Fig. 2.2). Therefore, fertilization did not induce early rooting of the cuttings, as most of the roots were produced at the end of the season. Root growth was unaffected by fertilization during at least the first 50 days of growth (first and second samplings took place at 34 and 53 days). Indeed, root length during the first two samplings was very low or negligible, despite the presence of fully grown ramets (Fig. 2.2).

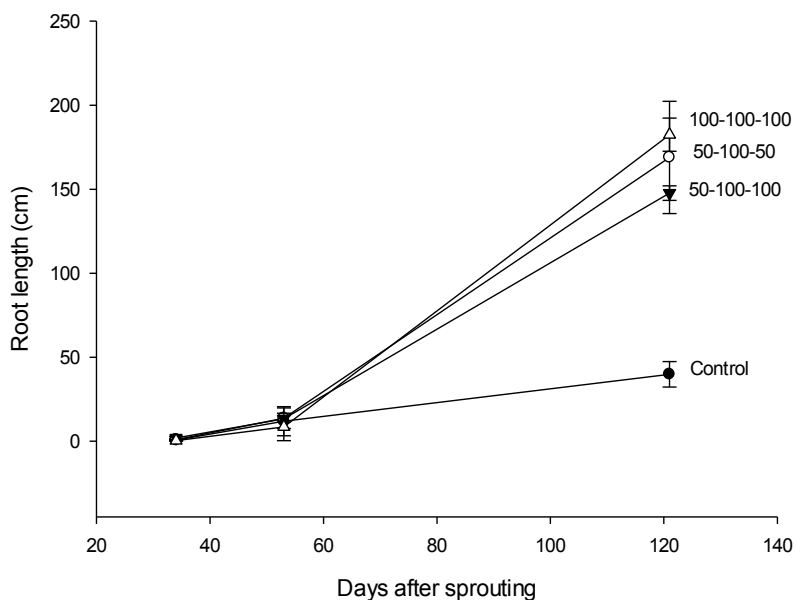
**Table 2.1** Results of ANOVA and a priori contrasts comparing the effects of the different fertilization treatments on plant growth and nutrient concentrations in the first and second growing season for cloudberry transplants of the second trial.

Year	Variable	$F_{3,11}$	$P$	Control vs Fertilized	100-100-100 vs 50-100-100	50-100-100 vs 50-100-50	
Foliar nutrients							
2014	Carbon	1.30	0.358	0.220	0.347	0.483	
	Nitrogen	8.27	<b>0.015</b>	<b>0.002</b>	0.853	0.284	
	Phosphorus	11.47	<b>0.007</b>	0.062	0.377	0.297	
	Potassium	6.67	<b>0.024</b>	<b>0.003</b>	0.510	0.212	
	Calcium	5.10	<b>0.043</b>	0.107	0.103	<b>0.029</b>	
	Sodium	3.46	0.092	<b>0.025</b>	0.962	0.427	
	Magnesium	2.16	0.194	0.881	0.225	0.100	
	Sulfur	7.38	<b>0.019</b>	<b>0.007</b>	<b>0.009</b>	0.133	
	Copper	0.24	0.866	0.621	0.603	0.748	
	Zinc	3.39	0.094	0.649	0.589	0.205	
	Manganese	1.81	0.246	0.741	0.967	0.056	
	Iron	5.10	<b>0.043</b>	0.454	0.683	0.959	
	Aluminum	1.82	0.245	0.111	0.371	0.315	
	2014	Root length	11.16	<b>0.007</b>	<b>0.000</b>	0.208	0.866
Rhizome mass		26.41	<b>0.001</b>	<b>0.002</b>	0.056	0.095	
Leaf area		3.66	0.083	<b>0.011</b>	0.239	0.316	
Number of buds		12.63	<b>0.005</b>	<b>0.001</b>	0.321	0.392	
Leaf area		5.99	0.031	<b>0.005</b>	0.114	0.167	
2015		Number of ramets per rhizome	16.17	0.003	<b>0.001</b>	0.222	0.067





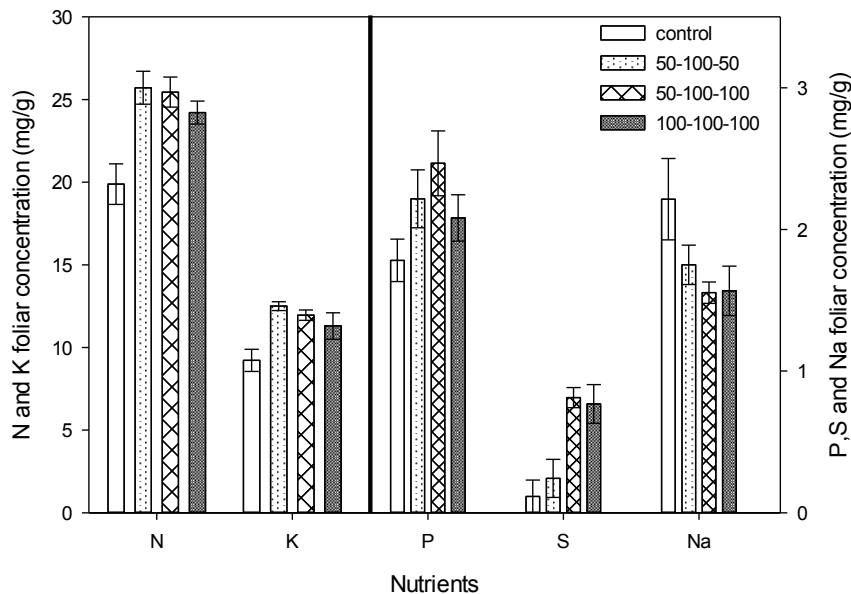
**Figure 2.1** Impact of different fertilization treatments on cloudberry root length (cm) at the final harvest. Mean  $\pm$  SE,  $N=3$ . Final harvest took place after 2 months during the first trial and after complete leaf senescence during the second trial.



**Figure 2.2** Root length (cm) progression in cloudberry during the first growing season for fertilized and control transplants. Mean  $\pm$  SE;  $N=3$ . Data are from the first growing season of the second trial.

Fertilization improved leaf concentrations of nitrogen, phosphorus, potassium and sulphur before any significant increase in root length took place (Table 2.1; Fig. 2.3). This response suggests that the rhizome is able to absorb some nutrient directly from the soil. Absorption of nutrients through the rhizome has already been reported for *Leymus chinensis* Trin. Tzvelev, a perennial rye grass (Liu et al., 2011). This species can absorb nitrogen directly through the rhizome in nutrient-poor environments, with nitrogen being preferentially transported to the shoot when uptake takes place in the rhizome. Nitrogen uptake by rhizomes has also been reported for *Carex bigelowii* (Brooker et al., 1999). Rhizome uptake could be a mechanism that has developed in non-mycorrhizal species to enhance nitrogen uptake in resource-poor environments (Brooker et al., 1999). Similarly, the rhizome of *Pteridium aquilinum* (L.) Kuhn is capable of taking up  $^{134}\text{Cs}$  and  $^{85}\text{Sr}$ , which are physiological analogues of calcium and potassium (Tyson et al., 1990). The seagrass *Zostera marina* L. is able to absorb phosphorus through its rhizomes, roots and leaves (Brix & Lyngby, 1985). However, what makes cloudberry somewhat unique is that these other species do not develop secondary growth on the rhizome. Therefore, it appears that even woody rhizomes can absorb nutrients directly.

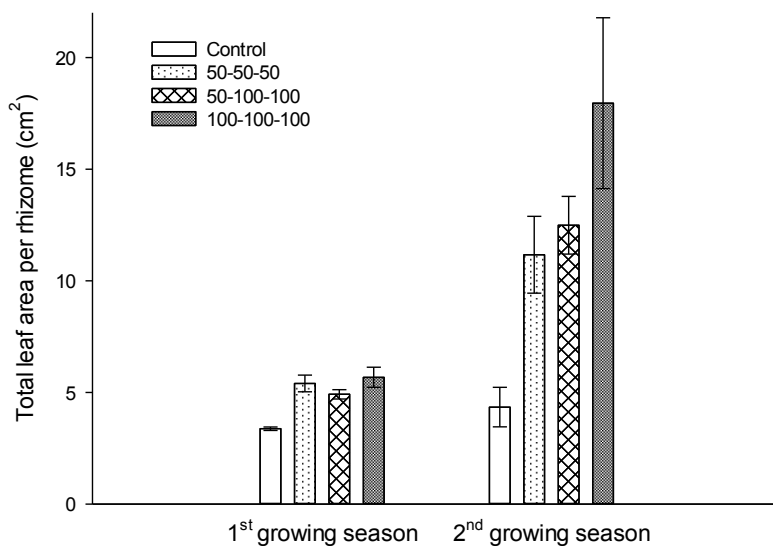
Contrarily to the other nutrients that accumulate to a greater extent in cloudberry leaves following fertilization, sodium foliar concentration was higher in control plots. Competition for adsorption sites is likely among nutrients on peat particles (Bolt et al., 1978), causing a decrease in sodium absorption in fertilized plants. According to the specific adsorption strength of the different nutrients (Millar & Turk, 1943), sodium would be replaced by ammonium or potassium in fertilized transplants.



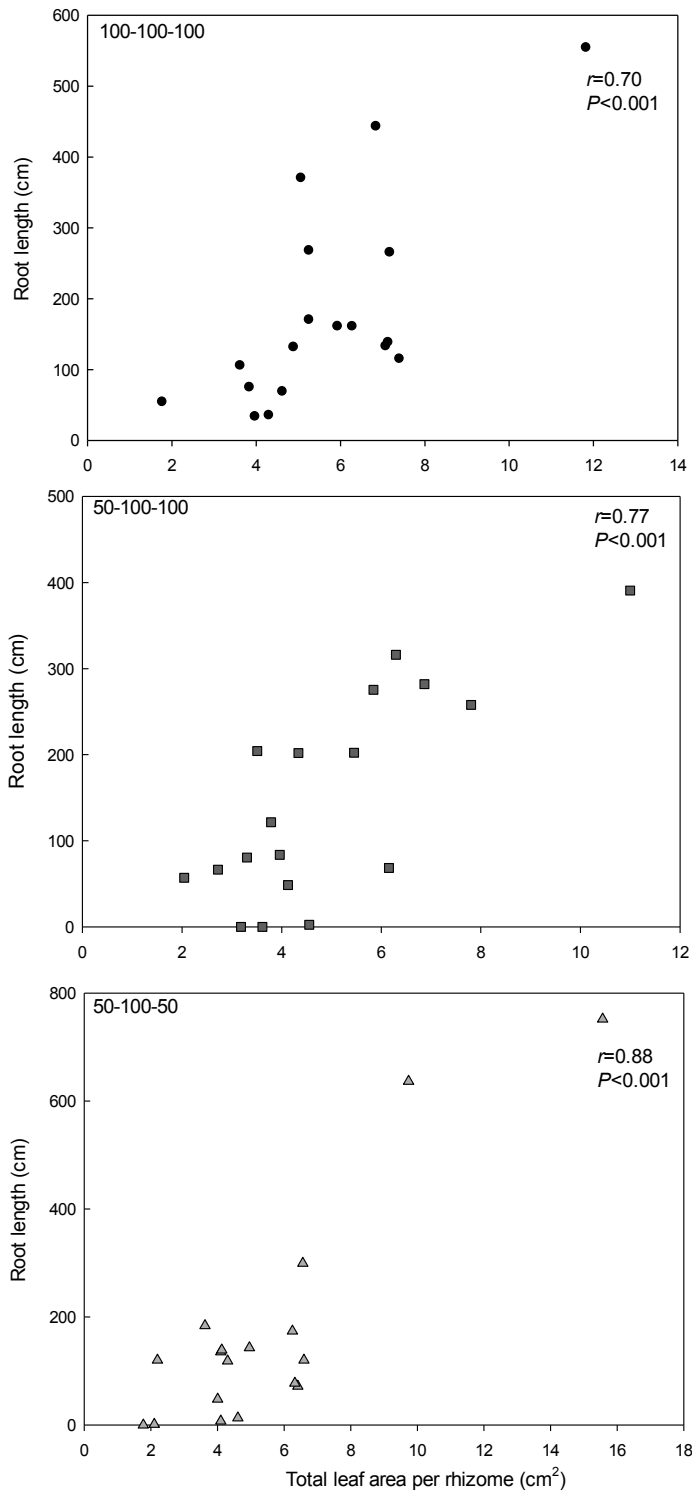
**Figure 2.3** Effects of mineral fertilization on foliar nutrient concentrations ( $\text{mg g}^{-1}$ ) in cloudberry transplants. Leaf samples collected in June and July were pooled before running the chemical analysis. Mean  $\pm$  SE.  $N = 3$ . Only nutrients for which at least two treatments differed are presented (see Table 2.1). Data are from the first season of the second trial.

Fertilization enhanced total leaf area produced per transplanted rhizome, but the effect was more apparent during the second growing season (Table 2.1; Fig. 2.4). Both the number of ramets and individual leaf size increased following fertilization. Higher foliar concentrations of nitrogen and larger leaves of the fertilized plants allow them to fix more carbon through photosynthesis (Evans, 1989). This extra carbon gain most likely allowed the fertilized transplants to produce more roots. Indeed, final root length was significantly correlated with total leaf area in each fertilizer treatment ( $P < 0.001$ ) (Fig. 2.5). Stepwise linear regression indicated that total leaf area ( $P < 0.001$ ) and leaf nitrogen concentration ( $P = 0.008$ ) are the most important factors explaining final root length ( $r^2 = 0.94$ ). Yet we cannot rule out the possibility that larger root systems were essentially attributable to the presence of fertilizers in the soil (Coutts & Philipson, 1977). In phosphorus-poor environments, such as peatlands (Damman, 1978), plants will not invest in root systems because the construction costs could outweigh the benefits that would be gained from absorbing phosphorus (Robinson, 1990). Therefore, the application of fertilizers with high levels of phosphorus could stimulate root production (Marschner, 2012). However, the delay in the production of a larger root system following the

application of fertilizers strongly suggests that root production is mainly driven or limited by the availability of carbohydrates rather than by the presence of fertilizers. In leafy rose (*Rosa hybrida* L. Madelon®) stem cuttings, rooting was delayed by low CO<sub>2</sub> concentrations, which led to low photosynthesis and low starch reserves in stems; rooting in rose thus appears to be limited by carbohydrate availability (Costal et al., 2007).

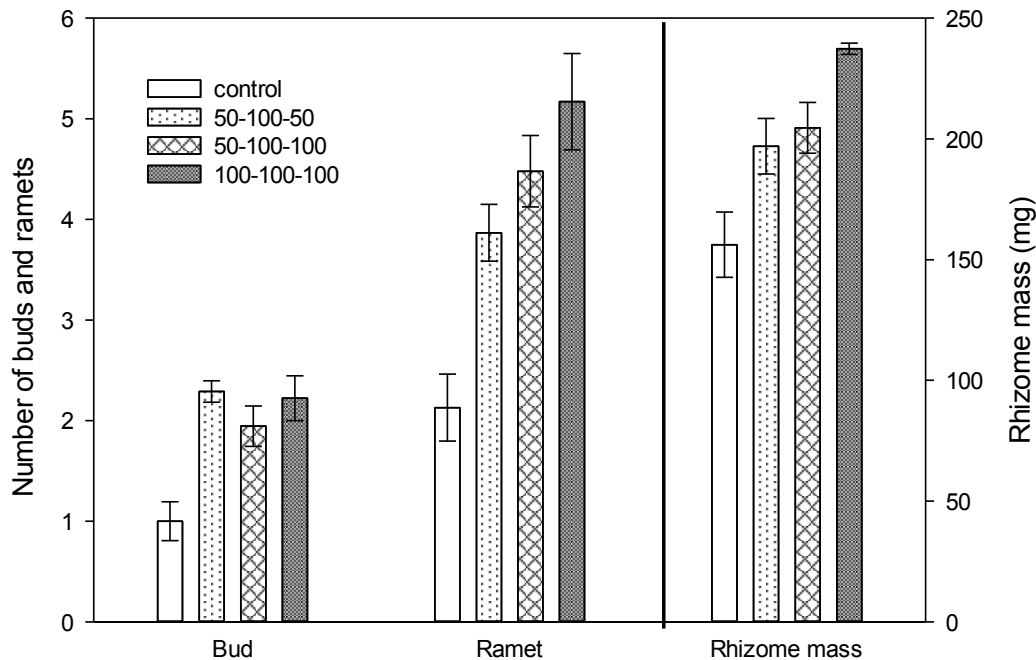


**Figure 2.4** Impact of mineral fertilization on total leaf area (cm<sup>2</sup>) produced per rhizome transplant during their first and second growing season; mean  $\pm$  SE,  $N=3$ . Data are from the second trial.



**Figure 2.5** Correlations between total leaf area per rhizome transplant (cm<sup>2</sup>) and total root length (cm) for the three fertilization treatments to which cloudberry transplants were subjected. Data are from the second trial.

Rhizomes from fertilized plots weighed more than those from control plots at the end of the season (Fig. 2.6), strongly suggesting that fertilization allowed the plant to store more carbohydrates during the season. These bigger rhizomes produced more buds at the end of the first growing season, that translated into a higher number of ramets during the second growing season, and which contributed to more leaf area produced per transplant. The larger rhizome mass at the end of the season could also mean more nutrient accumulation following leaf senescence and nutrient resorption (Rydin & Jeglum, 2013). It is worth mentioning that two good-sized fruits were produced in the fertilized plots during the second growing season, which is quite encouraging given that recently transplanted cloudberry very seldom produces fruits.



**Figure 2.6** Impact of mineral fertilization on the number of buds and rhizome mass (mg) at the end of the first growing season, and on the number of ramets produced during the second growing season in cloudberry transplants. Mean  $\pm$  SE.  $N=3$ . Data are from the second trial.

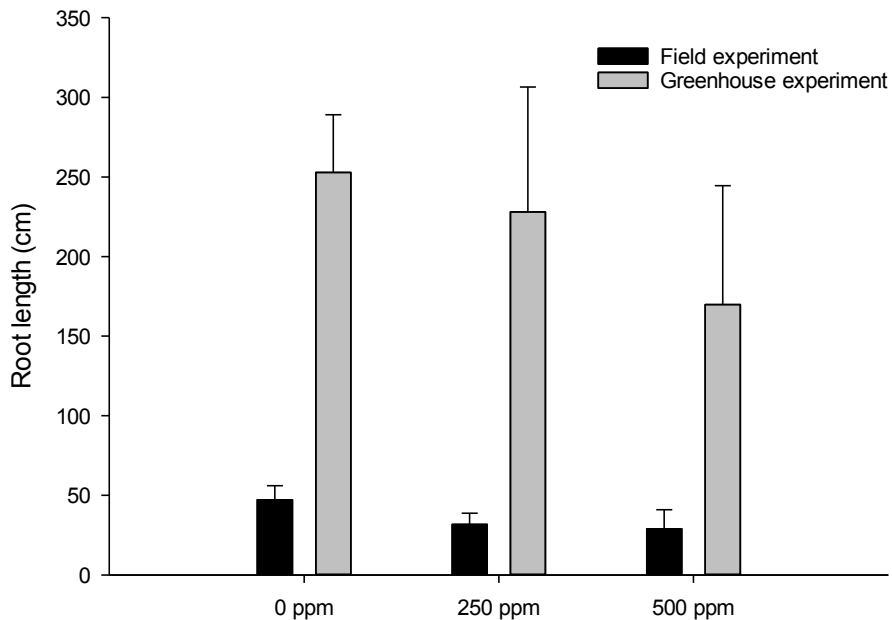
Fertilizer composition did not lead to any significant differences in root, leaf or rhizome growth. Cloudberry is usually co-limited by N and P (Hébert-Gentile et al., 2011), but a reduction in nitrogen content in the fertilizers did not negatively affect growth. Phosphorus nutrition appears to be

important for cloudberry growth, as plants exhibiting low growth and low fruit yield have lower leaf phosphorus concentrations (Gauci, 2008, Bussi eres et al., 2015). A deficiency in phosphorus can reduced the photosynthetic rates and, consequently, the growth rate of the plant (Ghannoum & Conroy, 2007). A reduction in photosynthesis would most likely lead to a reduction in carbohydrates, which appears to limit growth in cloudberry (Gauci et al., 2009).

### 2.5.3 Auxin Experiment

The application of auxins to the rhizome did not induce an early rooting, contrarily to what we initially posited. Auxin application causes high rhizome mortality, with the highest concentration (500 ppm) causing the highest mortality, followed by the intermediate concentration (250 ppm) in both greenhouse and field experiments. Transplants from the auxin treatments that survived did not produce longer roots than the controls. Application of auxin on cloudberry shoot clusters from meristem cultures stimulates the production of roots, but inhibits the production of new shoots (Martinussen et al., 2004). The application of auxins may have inhibited the development of auxiliary shoots on the rhizome by maintaining the bud in a state of quiescence, as shown on stem cuttings of others species (Srivastava, 2002). In the fertilization experiment, we showed that root production began after shoot production. Therefore, the inhibition of shoot production by auxin may explain the high mortality rate that was observed in the auxin-treated group. Development of callus was observed at the extremities of rhizomes grown in the greenhouse (pers. obs.). Growth hormones such as auxins can induce the development of callus (Ikeuchi et al., 2013). Such actively growing tissue may have depleted the carbohydrate reserves of the rhizomes incurring their mortality. Age of the rhizome segment could also have a negative impact on its rooting capacity and response to auxin treatment. Auxin application on mature petiole cuttings of *Hedera helix* L. can induce the formation of callus, which usually does not result in the formation of roots (Wesley, 1988). Rooting of rhizome segments of *Posidonia oceanica* (L.) Delile was enhanced by soaking the rhizome in a very low auxin concentration (5 ppm for 24 h). Indeed, prolonged exposure to a very small dose could be more effective in promoting root production along the whole rhizome without causing toxicity (Balestri & Lardicci, 2006).

Transplants grown in the greenhouse produced six times more roots than those grown in the field for similar season lengths ( $F_{3,11} = 19.7$ ,  $P < 0.001$ ; Fig. 2.7). The longer root system in plants that were grown in greenhouse is correlated with higher foliar surface area ( $r = 0.725$ ,  $P < 0.001$ ), as reported in the fertilization experiment. Growing conditions in the greenhouse, including a controlled temperature regime, regular watering and the absence of competition, appear to improve photosynthetic rates and the growth of the plant.



**Figure 2.7** Impact of auxin treatments (K-IBA) on root length (cm) at the end of the first growing season in cloudberry rhizome transplants. Transplants were either grown in the field or in the greenhouse. Mean  $\pm$  SE.  $N=7$  for the greenhouse experiment and  $N=5$  for the field experiment.

## 2.6 Conclusion

Mineral fertilization stimulated root growth and elongation, and increased the total leaf area of the transplants after a single growing season. Yet fertilization did not promote early rooting. Nutrients appear to be absorbed by the lignified rhizome and used for leaf production well ahead of root production. Once all leaves are fully mature, photosynthates are most likely translocated to the rhizome and roots, which stimulates their growth. The survival of rhizome transplants remains low and variable despite the overall positive effect of mineral fertilization. In the absence of significant



differences among fertilizers, either formulation could be applied until trials with new combinations of nutrients further improve cloudberry growth. A long-term follow-up will be necessary to quantify the effects of a larger root system on plant propagation and fruit yield. Auxin, at the concentrations tested, caused high mortality and did not stimulate root growth. Simultaneous greenhouse and field experiments using rhizome transplants from the same source confirm that cloudberry produces many more roots when grown under greenhouse conditions. Fertilization at planting is recommended to improve shoot and root growth of the new transplants.

**Chapitre 3. Low fruit yields in cloudberry are not associated with low nutrient absorption but rather to high levels of Mn, Fe, Cu and S.**

### 3.1 Résumé

La chicouté (*Rubus chamaemorus*) est une espèce circumpolaire qui pousse dans les tourbières ombrotrophes. Le rendement en fruits de la chicouté est variable d'une année à l'autre et d'un site à l'autre. Des déséquilibres nutritifs sont soupçonnés d'être la cause des faibles rendements en fruits observés dans certaines populations. L'objectif de l'étude était de quantifier les changements saisonniers dans les nutriments foliaires chez les plants végétatifs et fructifères de chicouté et d'identifier les déséquilibres nutritionnels chez des populations de l'Est du Canada. Des feuilles ont été échantillonnées toutes les deux semaines durant toute la saison de croissance dans huit tourbières. Trente-deux parcelles ont également été mises en place dans ces huit tourbières afin de déterminer leurs rendements en fruits et des feuilles provenant de ces parcelles ont été prélevées durant le développement des fruits. Les données de concentrations de nutriments foliaires ont été analysées avec une approche compositionnelle qui permet de relier le rendement en fruits avec les balances nutritionnelles. Les balances nutritionnelles qui diffèrent entre les parcelles productives et les parcelles à faible rendement sont [P,Mg,K,Ca|S,N]; [S|N]; [Zn|Cu] et [Al|Mn,Fe]. Les parcelles à faibles rendements accumulent plus de S, Cu, Mn et Fe que les parcelles productives. L'échantillonnage foliaire aux deux semaines a montré que les concentrations de N, P, K, S, Zn et Cu diminuent durant la saison tandis que celles de Ca, Mg, Mn et Fe augmentent. Les ramets fructifères et végétatifs présentaient des concentrations en nutriments foliaires similaires et ce tout au long de la saison.

Les plus fortes concentrations foliaires de Cu, Mn, Fe dans les plantes à faibles rendements pourraient être reliées à la stratégie de relâchement des carboxylates par les racines tels que décrit par Lambers(2015). Par ailleurs, les concentrations plus élevées en S dans ces plants pourraient refléter la mise en place d'une stratégie de détoxification des métaux tels que le Cu. Il serait maintenant approprié de tester des traitements de fertilisation spécifique afin de rétablir les balances nutritionnelles dans les secteurs à faibles rendements.

### 3.2 Abstract

Cloudberry (*Rubus chamaemorus*) is a circumpolar species growing in ombrotrophic peatlands. Cloudberry fruit yield is variable from year to year but also on a spatial basis. Nutritional imbalances are suspected of causing the low yields observed in some populations. The objective of the study was to quantify the seasonal changes in cloudberry foliar nutrients of vegetative and fruiting ramets and uncover potential nutrient imbalances in populations located in eastern Canada. We harvested leaves every two weeks throughout the growing season in eight peatlands. Likewise, 32 plots were established inside these eight peatlands to monitor fruit yield, and leaves were harvested during fruit development in each plot. Foliar nutrient concentrations were analyzed using a compositional approach that links fruit yields to foliar nutrient balances. The nutrient balances that differed between productive plots and low yield plots are [P,Mg,K,Ca|S,N]; [S|N]; [Zn|Cu] and [Al|Mn,Fe]. Low yield plots accumulate more S, Cu, Mn and Fe than high yield plots. The bimonthly leaf sampling indicates that N, P, K, S, Zn and Cu decreased during the season while Ca, Mg, Mn and Fe increased. Throughout the season, fruiting and non fruiting ramets exhibited similar foliar nutrients concentrations.

The higher foliar concentrations of Cu, Mn and Fe in low yield plot could be linked to the carboxylate release strategy as described by Lambers (2015). Furthermore, the presence of higher concentration of S in the leaves in low-yield plots could reflect a strategy to detoxify metals such as Cu. Specific fertilization treatments will need to be investigated in order to re-establish nutrient balances in low yield plots.

### 3.3 Introduction

Cloudberry (*Rubus chamaemorus*) is a small perennial plant producing amber berry. This species grows in ombrotrophic peatlands of the circumpolar regions (Resvoll, 1929). Cloudberry has a high economic value and it is already well commercialized in Scandinavia (Saastamoinen et al., 2000b) whereas it is just starting to appear on the market in Canada. The berry is harvested in natural peatlands; to our knowledge there is no commercial cultivation neither in Canada nor in Scandinavia. Fruit yield is very variable from year to year and among sites (Resvoll, 1929, Small & Catling, 2000). Variable yields are due to external factors such as late frost or insufficient pollination (Ågren et al., 1986, Kortesharju, 1988), but fruit productivity can also be affected by a limitation in nutrients. Ombrotrophic peatlands (bog) have low nutrient supply, as nutrients only come from precipitations (Damman, 1978). Nutrients derived from rocks such as phosphorus, potassium and many micronutrients are in low concentrations in peatlands (Rabenhorst & Swanson, 2000).

Slow-growing species such as cloudberry does not show visual signs of nutrient limitations (deficiency); these plants reduce their growth in response to a reduction in nutrients without apparent symptoms (Chapin, 1980). The only way to find out which nutrient are limiting is to refer to leaf analysis (Bould, 1968). Too often, however, only N, P and K are analyzed. Recent studies on cloudberry mineral nutrition have shown that micronutrients appear to be responsible for low fruit productivity (Parent et al., 2013, Bussi eres et al., 2015).

It is well known that phenological stages and reproductive status can influence foliar nutrient concentrations (Marschner, 2012). Therefore, nutrient analysis needs to be performed throughout the season to characterize how the different nutrients evolve in a given species. Fruit production can also influence foliar nutrient concentration as mobile nutrients like N, P, K and Mg are translocated from leaves to developing fruits (Moreira & Fageria, 2009). Comparing fruiting and non-fruiting shoots can help identify nutrients that become limiting during fruiting.

The use of individual nutrient concentrations for nutrient diagnostic leads to bias due to their non-independence. Foliar nutrient concentrations are linked to each other: an increase in the abundance of one nutrient will dilute the concentration of another nutrient in the leaves (Parent et al., 2012).. The

compositional nutrient diagnostic (CND) with orthogonal nutrient balances avoids this analytical problem (Parent et al., 2012). CND analyzes nutrient balances as isometric log ratios (*ilr*) of experimental plots in relation to their productivity to identify nutrient balances that are related to yield. A maximum number of D-1 nutrient balances can be analyzed in a D-part composition. Those balances are chosen to represent nutrient relationship of interest for a given species or a given type of soil. A previous CND analysis has been performed on cloudberry populations from the Québec North-Shore, in Eastern Canada to identify nutrient toxicity or limitations (Parent et al., 2013) but populations from different regions can exhibit different nutrient limitations.

The main objective of the present study was to determine the nutrients that limit yield in New-Brunswick natural populations (Eastern Canada), using the CND approach and to compare those limitations with the nutrients limitations reported for Québec North Shore populations. We performed sequential foliar harvests to characterize nutrient evolution through the season in both fruiting and vegetative ramets to help identify specific nutrients that might be limiting during cloudberry fruit production. Determining the evolution of nutrients through time will also allow us to recommend a specific phenological stage for leaf harvest in order to standardize foliar nutrient analyses among studies for this species.

### **3.4 Material and methods**

#### 3.4.1 Site description

This study was conducted in the Acadian peninsula, in the North-East of New-Brunswick, Eastern Canada (47°45'N, 64°43'W). Eight natural ombrotrophic peatlands were selected over 2 years (2013 and 2014) for their variable abundance of female ramets (Annexe 2). Typical vegetation in these sectors included the presence of a continuous sphagnum carpet, and the presence of *Empetrum nigrum*, *Ledum groenlandicum*, *Vaccinium angustifolium*, *Vaccinium oxycoccus*, *Chamaedaphne calyculata*, *Kalmia angustiflora* and *Eriophorum* sp.

#### 3.4.2 Compositional Nutrient Diagnostic

*Sampling:* In 2013 and 2014, thirty-two plots of one m<sup>2</sup> presenting a range of female ramets densities were set up in the eight natural peatlands selected, that is four plots per site. In each plot, the number of flowers and fruits were counted, and the fruits were harvested when ripe and weighed. Fifteen leaves from fruit-bearing ramets were collected in each plot on July 20 and July 21 during fructification.

*Data Analysis:* The compositional data were analyzed using the compositional nutrient diagnostic (CND) developed by Parent et al. (2013) and tested with cloudberry tissues. Thirteen elements were included in the analyze: 12 common nutrients including carbon (C) and a filling value (Fv) which represents the remaining leaf composition (O and H) in percent, which allow to test twelve nutrients balances. These balances also need to be orthogonal. The twelve balances were set up taking into account what we have learned from previous nutrient analysis in cloudberry (Parent et al., 2013, Bussi eres et al., 2015) and the nutrient limitations that are most likely to occur in the acidic organic soils of ombrotrophic peatlands. The first two balances contrast Fv to all nutrients and carbon to all nutrients. The macronutrients (N,P,K,S,Mg and Ca) were compared to metals (Al, Mn, Fe, Zn and Cu), knowing that some of these metals appear to accumulate in the leaves of cloudberry. We then tested within macronutrients, the balance P,K | Mg,Ca, as Mg and Ca are less limiting in peatlands than P and K despite their general low concentrations (Campbell & Rochefort, 2001). Previous studies have reported that S accumulates in low yield plants (Parent et al., 2013). We thereafter tested the S|N balance to determine the relationship between S accumulation and protein synthesis as S is mostly found in two amino acids (Marschner, 2012). Al, Mn and Fe are more available in low soil pH and were contrasted with Cu and Zn which are in very low concentration in peat (Andersen et al., 2011). Zn concentration was then contrasted with that of Cu. We have reported some very high Mn concentration in cloudberry leaves (Bussi eres et al., 2015) which could be related to a carboxylate-releasing strategy put in place by the plant to limit the absorption of Al (Wang et al., 2007, Lambers et al., 2015). Therefore, Al concentration was compared to that of Mn and Fe. Those 12 mineral balances were linked to the plot yield to identify balances associated with low yield.

Nutrient balances are expressed using isometric log ratios (*ilrs*) calculated using this equation,

$$ilr_i = \sqrt{\frac{ni^+ ni^-}{ni^+ + ni^-}} \ln \frac{g(ci^+)}{g(ci^-)}$$
, where  $n^-$  and  $n^+$  are respectively the nutrients to the left and to the right of the nutrient balance (Annexe 3) and  $g(ci^-)$  and  $g(ci^+)$  are the geometrical means of the nutrients at the

left and at the right of the balance. A positive *ilr* means that the nutrient concentration on the right side of the balance weights more than that of the nutrients on the left. For example, if N concentration in the S|N balance increases, the balance will lean to the right due to the heaviest weight of N and the *ilr* of this balance will increase. We set a fruit yield threshold of 100 kg ha<sup>-1</sup> for the productive plots. The plots were then partitioned according to their yield and Mahalanobis distance threshold. Mahalanobis distance is a measure of multivariate distance which allows to identify plots with outliers *ilrs*. The plots were separated into four groups; plots with low yield and imbalanced nutrients (TP for true positive, nutrient imbalance), plots with good yield and balanced nutrients (TN for true negative, nutrient balance), plots with high yield but presenting nutrient imbalances (FP for false positive) and plots with low yield but identified as balanced (FN for false negative). Then a Tuckey test between TN and TP plots was used to target the nutrient balances associated with low yield. For more details on this analysis see Parent et al. (2013).

### 3.4.3 Bimonthly Nutritional Portrait

*Sampling:* During 2013, four sectors were selected in four different natural peatlands while in 2014 five new sectors were visited in five peatlands, one of which had been visited the previous year. Each two weeks during the growing season (i.e. five sampling dates) a sample composed of fifteen leaves was collected on vegetative ramets and another one on female fruiting ramets. The diagonal of each leaf was measured and used to calculate leaf area using the following equation: Leaf area (cm<sup>2</sup>) =  $0.5242 \exp^{0.7158 * \text{Diagonal}}$  (Théroux-Rancourt et al., 2009).

*Data Analysis:* We used an ANOVA with random factors (years) to test the effect of the type of ramets (fruiting and vegetative ramets) and time of sampling on the twelve nutrients using MIXED model in SAS program (SAS program). Data were transformed when needed to respect normality and homogeneity of variance; a log transformation was applied on P and Zn concentrations and a square root transformation was applied for N, Cu and Fe data. When results of ANOVA were significant, we applied a multiple comparison with a least-square means and Tuckey-Kramer adjustment.



### 3.4.4 Foliar Analysis

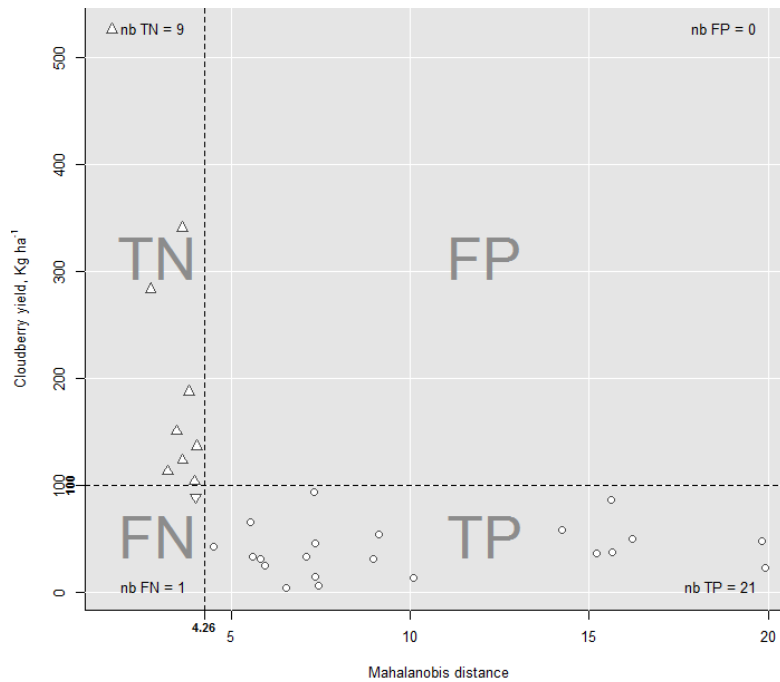
Leaves from the two experiments were analyzed using the same method. Leaves were first dried at 65°C for 48 hours in an oven, then ground. The concentration of C, N and S was obtained by combustion with a Leco CNS-2000 using subsamples. The rest of the tissues were digested with perchloric and nitric acids prior to quantify their nutrient concentrations (P, K, Mg, Ca, Al, Fe, Mn, Zn, Cu) by plasma emission spectroscopy (ICP-OES) (Barnhisel & Bertshc, 1982).

## 3.5 Results

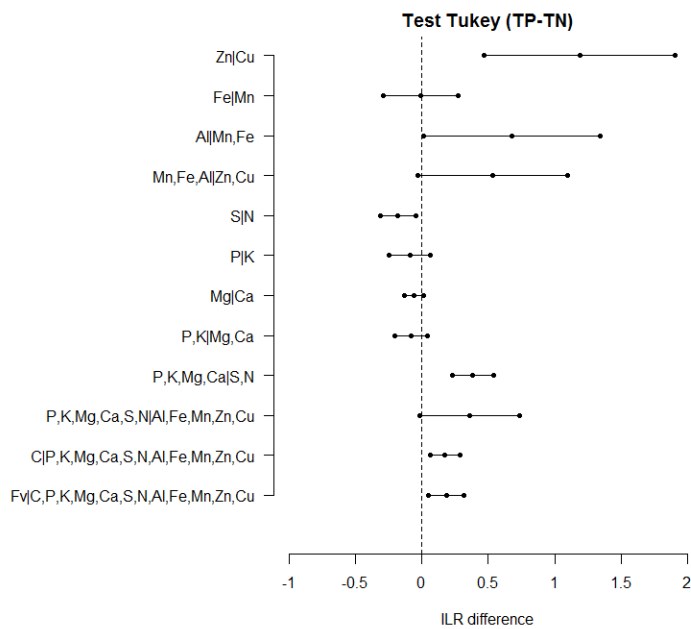
### 3.5.1 Compositional Nutrient Diagnostic

The yield estimated from the 1 m<sup>2</sup> plots varied between 0.4 and 52 g m<sup>-2</sup> (4 to 520 kg ha<sup>-1</sup>). The yield threshold of 100 kg ha<sup>-1</sup> determined for this data set corresponds to the 75 quantile of all 31 plots used in the analysis. A plot was removed from the initial data set due to an abnormal value of carbon foliar concentration.

The analysis classified plots into 9 true negative (TN), 21 true positive (TP) and 1 false negative (FN) (Fig. 3.1). The high accuracy of the test (97%) is explained by the low number of FN and the absence of FP. The FN represent a plot with low yield and identified as balanced; external factors such as late frost or deficient pollination might explain this classification. The Tuckey test between the nutrient balances of TN and TP plots revealed which nutrient balances varied with cloudberry yield (Fig. 3.2). Six nutrients balances differed significantly between TP and TN plots: [Zn|Cu] ( $P<0.005$ ), [Al|Mn,Fe] ( $P<0.05$ ), [S|N] ( $P<0.01$ ), [P,Mg,K,Ca|S,N] ( $P<0.001$ ), [C|nutrients] ( $P<0.005$ ) and [Fv|C+Nutrients] ( $P<0.05$ ).

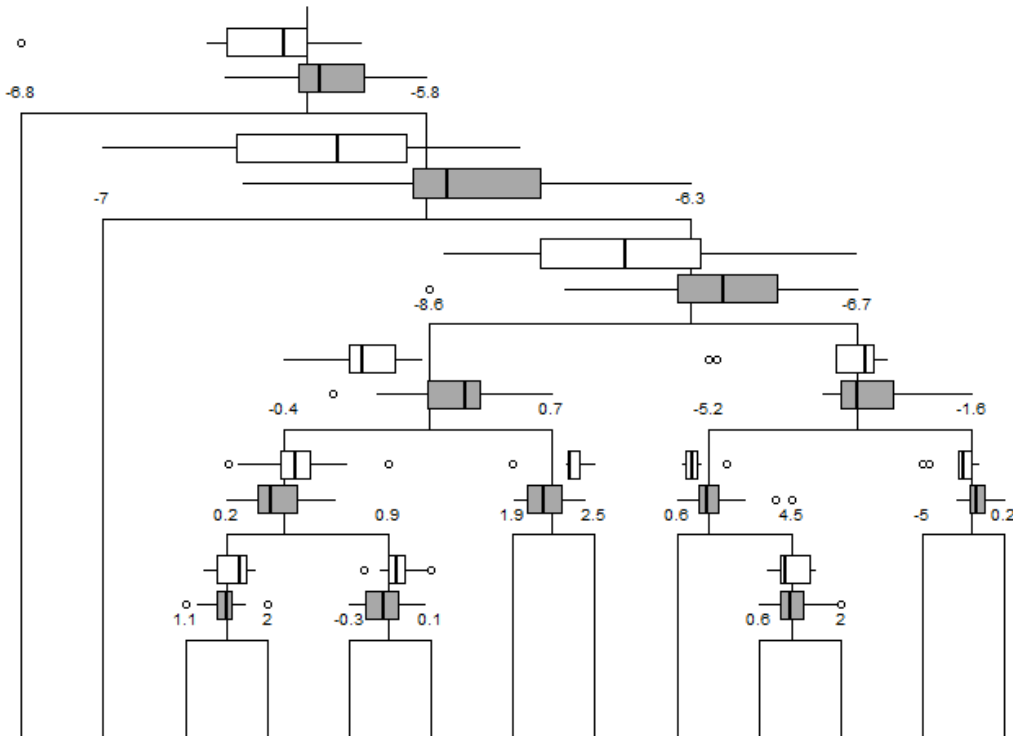


**Figure 3.1** Binary classification of cloudberry fruit yield and Mahalanobis distance of the *ilr* balances for the 31 plots.



**Figure 3.2** Results of Tukey tests comparing *ilrs* of TP and TN plots. *ilr* difference is significant when its range does not overlap with zero ( $P < 0.05$ ). Negative *ilr* ranges indicate that the left side of the balance weight more than the right side in TP (low yield) plots compared to the balance calculated for TN plots.

Low yield plants accumulated more nutrients relatively to carbon and to the filling value (Fv; Fig. 3.3). The accumulation of Cu relatively to Zn and of S relatively to N seemed to affect the yield negatively. Low yield plants also absorbed more Mn and Fe relatively to Al. Leaves from plots with low yield contain more S and N relatively to P, K, Mg and Ca.



	Fv	C	P	K	Mg	Ca	S	N	Al	Fe	Mn	Zn	Cu
TN	488	476	0.85	8.66	4.52	4.06	0.67	16.6	0.0462	0.081	0.491	0.0329	0.00134
TP	480	481	0.92	8.29	4.44	3.69	1.02	20.0	0.0374	0.128	0.742	0.0267	0.00303
FN	476	491	0.96	7.07	4.29	3.43	0.51	16.1	0.0374	0.058	0.549	0.0453	0.00174

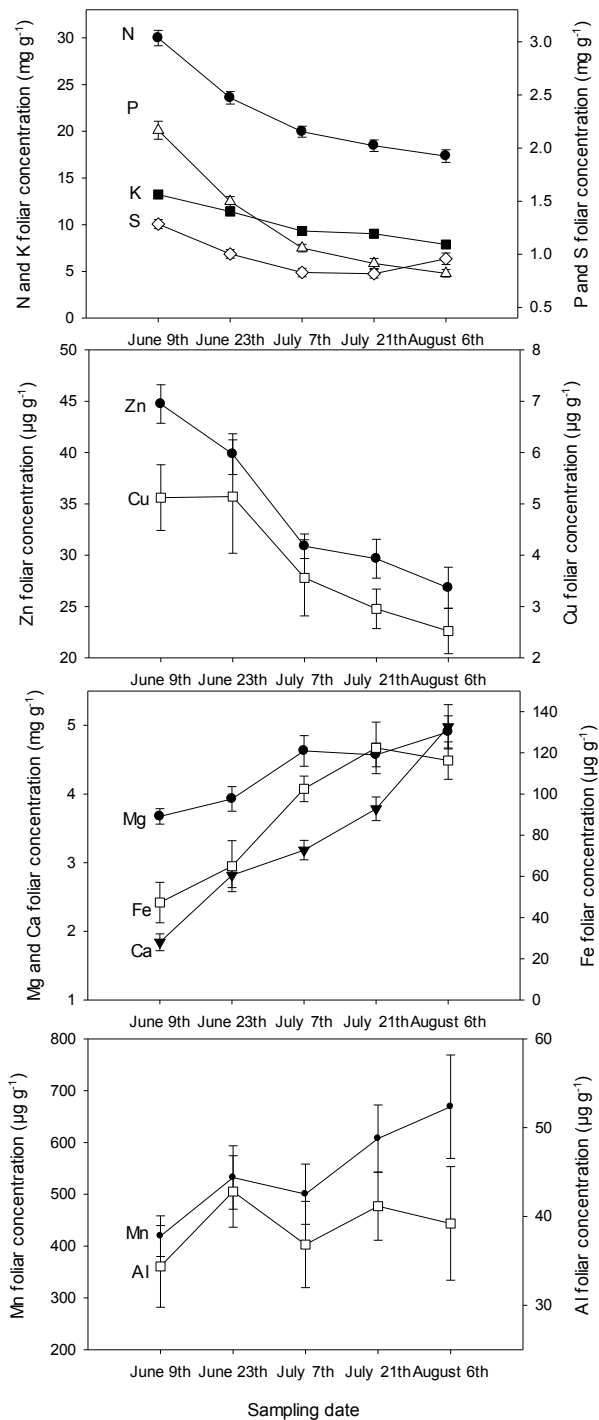
**Figure 3.3** Dendrogram of nutrient balances with boxplot representing the distribution of *ilrs* among the plots classed as TP or TN. Grey boxplots symbolize TP plots and white boxplots symbolizes TN plots. The table contains mean foliar nutrient concentrations in  $\text{mg g}^{-1}$  for TN, TP and FN plots.

### 3.5.2 Bimonthly Nutritional Portrait

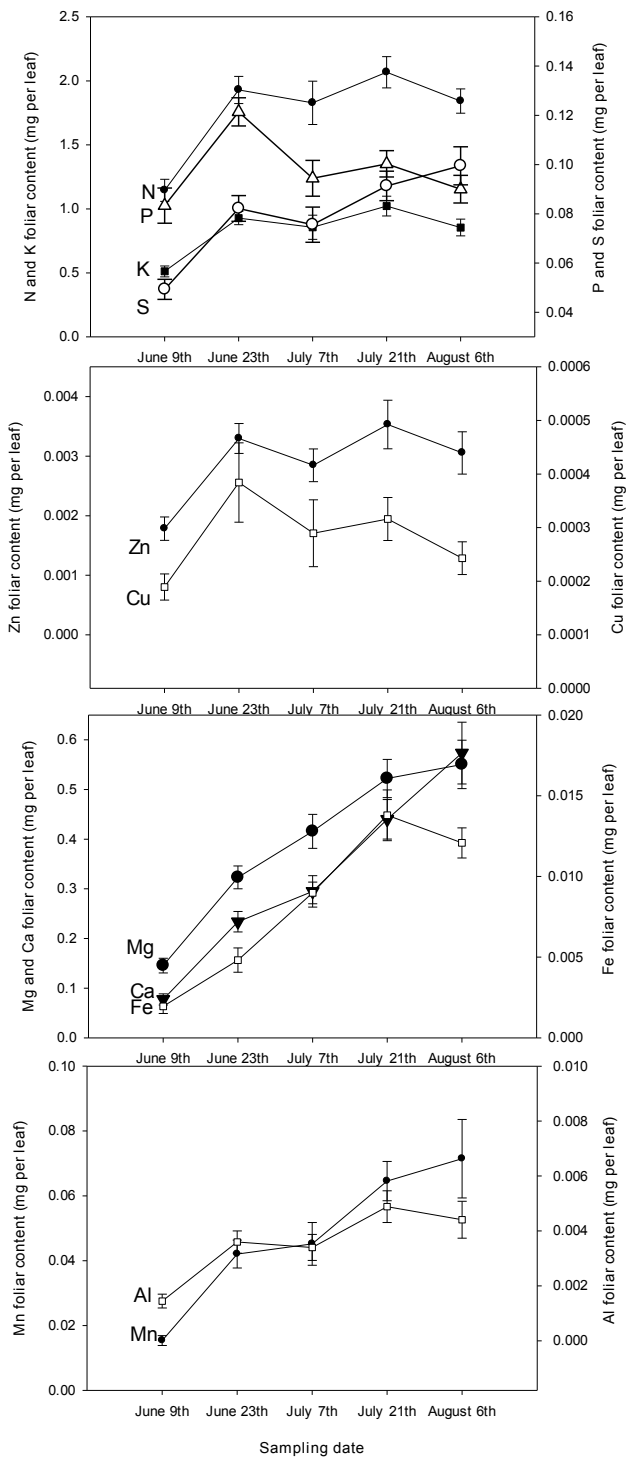
No differences in nutrient concentrations were found between vegetative and fruiting ramets. Nutrient foliar concentration was influenced by sampling date for all nutrients except Al and C. Foliar

concentration decreased during the season for N, P, K, S, Zn and Cu whereas it increased through time for Mg, Ca, Fe and Mn (Fig. 3.4).

Total foliar content was calculated by multiplying the foliar concentration with the leaf dry mass. Total foliar content of C (data not shown), Mg, Ca, Fe, Al, Mn and S increased in the leaves throughout the season. Total foliar content of the other nutrients (N, K, Zn and Cu) increased during leaf expansion early in the season and then remained constant during the rest of the summer, whereas P total content decreased after leaf expansion was completed (Fig. 3.5).



**Figure 3.4** Concentrations of 11 nutrients in cloudberry leaves throughout the season of 2013 and 2014. The first sampling took place in early June, then every two weeks until the end of fruit maturation. Mean  $\pm$  SE.  $N=18$ .



**Figure 3.5** Total foliar content (mg per leaf) of 11 nutrients in cloudberry leaves throughout the season of 2013 and 2014. The first sampling took place in early June, then every two weeks until the end of fruit maturation. Mean  $\pm$  SE.  $N=18$ .

### 3.6 Discussion

The compositional nutrient diagnostic has allowed to classify all but one plot as either high yield or low yield plots. The misclassified plot produced fruits but they were completely dry or mouldy at the time of harvest, which explains their low yield despite presenting balanced nutrients. The high yield plots differ from low yield plots for six different nutrient balances. Low yield in cloudberry seems mostly related to imbalances involving micronutrients rather than macronutrients, and more often than expected these imbalances appear to be associated with accumulation of some nutrients rather than to a lack of it. For example, low yield plants had higher concentration of S, Mn, Fe and Cu than high yield plants. Sulphur is also accumulating in low yield plants as reported previously in cloudberry from another region (Parent et al., 2013). The accumulation of micronutrients in low yield plots might explain the inefficiency of different fertilization trials that have been conducted over the years in cloudberry (Østgård, 1964, Taylor, 1971, Hébert-Gentile et al., 2011). Indeed, fertilization experiments essentially added macronutrients in an attempt to increase fruit production, but the low yield in cloudberry seems mostly caused by micronutrient toxicity, most likely related to the very acid edaphic conditions where it grows.

Seasonal changes in foliar nutrient concentrations were large and showed opposite trends among nutrients. The seasonal decrease of N, P and K has been reported in many species (Guha & Mitchell, 1966, Grigal et al., 1976, Dominguez et al., 2015). Foliar concentration of S is rarely analyzed, and thus no seasonal trend has been reported. In the case of cloudberry it appears that S concentration followed the trend observed for the other main macronutrients (N,P,K) except for the slight increase observed at the end of the season. Seasonal change in Zn concentration is not constant over species (Gjengedal, 1996) while Cu concentration tends to decrease during the season (Gjengedal, 1996, Viers et al., 2013). The Zn uptake can be reduced in low pH soil which can explain the seasonal decrease in cloudberry leaves (Gjengedal, 1996). Calcium is largely known to increase during the season in leaf tissues due to passive accumulation through the transpiration stream (Chapin, 1980). An accumulation of Mg is reported in some studies (Viers et al., 2013, Dominguez et al., 2015) but a seasonal decreased of Mg has also been seen in some shrubs (Grigal et al., 1976). The increase in Fe concentration during the season is not common but it has been reported in some varieties of grapes (Dominguez et al., 2015) and in some trees (Guha & Mitchell, 1966). The concentration of Mn is increasing during the season in many species: *Acer pseudoplatanus*, *Larix gmelinii*, *Vitis vinefera*

(Guha & Mitchell, 1966, Viers et al., 2013, Dominguez et al., 2015). According to the seasonal change in foliar nutrient concentration we recommend to sample leaves during fructification (between early July and late July), as nutrient concentrations are more stable than during the unfolding and the flowering, i.e in June.

Fruiting and vegetative ramets exhibited similar foliar nutrient concentrations throughout the season, infirming our hypothesis. It appears that the higher nutrient and carbohydrate demand for fruit production in female ramet did not influence the nutrients concentrations in leaves in comparison to vegetative ramet. Jean and Lapointe (2001) showed that defoliation of the fruiting ramet did not impact fruit production, and concluded that the carbon necessary for fruit production can come from the rhizome or from other ramets via the rhizome system, in absence of leaves. We posit that nutrients can also be imported from the rhizome or from vegetative ramets to meet nutrients needed for fruit development which would explain the absence of difference between nutrient concentration in leaves of vegetative and reproductive ramets.

The imbalance in Al|Mn,Fe in low yield plants appears to be due to an accumulation of Mn despite its low availability in organic soils (Rabenhorst & Swanson, 2000). All plots exhibited high foliar concentration of Mn, ranging from 257 to 1685  $\mu\text{g g}^{-1}$ , while a foliar concentration of 50  $\mu\text{g g}^{-1}$  is considered sufficient for optimum growth (Epstein & Bloom, 2005). Low yield plants accumulated higher concentrations of Mn (373 to 1685  $\mu\text{g g}^{-1}$ ), but lower Al concentration than high yield plants. High Mn concentrations were also found in cloudberry leaves of plants grown in fibric peat (slightly decomposed peat) (Bussi eres et al., 2015).

The higher concentrations of Mn in low yield plants can be due to the release of carboxylates in the vicinity of roots in response to Al soil concentration. Indeed, leaf Mn accumulation has recently been associated with this strategy (Lambers et al., 2015). In acidic nutriment-impooverished soils like peatlands, the number of mycorrhizal species is diminished but diverse nutrient acquisition strategies such as the release of carboxylates are found (Oliveira et al., 2015). Roots could release carboxylates in response to two different situations: when Al concentration is high or when P availability is low in the soil (Wang et al., 2007). Al-induced carboxylates release was more rapid than carboxylate release in response to low P availability (Wang et al., 2007). The carboxylates mobilize P



bound to oxides and hydroxides of Fe and Al. Carboxylates can also mobilize some metal cations such as Fe and Mn, whereas they chelate Al. Sphagnum bogs having low P availability and cloudberry being particularly sensitive to Al, it would seem logical that this species use the carboxylate-releasing strategy in order to improve P absorption and reduces Al availability.

Results from a previous study which took place in a greenhouse also suggest that cloudberry roots release carboxylates (Bussi eres et al., 2015). However, contrary to the present results, it was the high yield plants which exhibited high foliar Mn concentrations. The release of carboxylates should increase plant productivity by either limiting the toxicity of Al or by supplying P to the plant. However, exudation of carbon molecules linked with the strategy can be costly for a source-limited species such as cloudberry (Gauci et al., 2009, Marschner, 2012) and might explain the low yield of plants that appear to rely on this strategy in the field. Plants grown under greenhouse conditions seem to be less carbon-limited than plants growing in field conditions (chapter 2), which could explain the beneficial effect of releasing carboxylate under greenhouse growth conditions.

Leaves accumulated Mn and Fe during the season whereas the increase in Al concentration was much more modest; these results are also consistent with a carboxylate-releasing strategy which immobilizes Al in the soil but releases Mn and Fe. But cloudberry does not seem to rely on this strategy under all growing conditions. In the study conducted by Parent et al. (2013), Mn concentration was half that reported in the present study and low yield were associated with higher leaf Al concentrations, not with higher Mn concentrations suggesting that the plant did not exudate carboxylates, or at least not the same extent as in the present study.

Low P availability can also trigger the release of carboxylates by the roots to mobilize P bound on Al and Fe oxides and hydroxides (Lambers et al., 2015). No correlations were found between the Mn and P foliar concentrations (data not shown), nor in the studies of Oliveira et al. (2015) and Hayes et al. (2014) . However, P is rapidly used in plants particularly during fruiting (Mengel & Kirkby, 1978) and thus an increase in P absorption might not translate into higher P in leaf tissues. Indeed, foliar P content decrease in leaves at the time fruit starts to develop in early July (Fig. 3.5). Leaf P concentration is lower in New-Brunswick plots ( $0.91 \text{ mg g}^{-1}$ ) than in Qu ebec North Shore ( $1.39 \text{ mg g}^{-1}$ ), and could reflect the general P availability in the peat. However, the absence of soil analysis from

the New-Brunswick plots preclude us from determining if the carboxylate-releasing strategy was triggered by low phosphorus availability or by aluminum toxicity.

Sulfur is identified as another macronutrient causing an imbalance, as previously reported in cloudberry (Parent et al., 2013). Uptake of N and S are strongly linked, both nutrients being incorporated into amino acids (Epstein & Bloom, 2005). Indeed, 90% of organic S is usually present in amino acids (Lambers et al., 1985). Low yield plants exhibited a higher S/N ratio in their leaves. S is absorbed throughout the season while N is mainly absorbed during leaf unfolding (Fig. 3.5). The foliar S concentration even increases at the end of the season. Sulfur can be toxic when present in the form of sulfide following sulfate reduction under flooded soil (Blodau et al., 2007, Martin & Maricle, 2015). However, cloudberry rhizomes and roots usually occupy the acrotelm (Taylor, 1971) and are thus exposed to flooding conditions only for short periods of time. S uptake can be increased in response to metal toxicity (Nocito et al., 2006). Indeed the low yield plants exhibit an imbalance in favour of micronutrients [P, Mg, K, Ca, S, N | Al, Fe, Mn, Zn, Cu], although this imbalance was not significant ( $P=0.062$ ). Accumulation of S in low yield plants could also explain the imbalance of the P, K, Mg, Ca | S, N ratio and of the C | Nutrients ratio.

Higher Cu concentration in low yield plants also impacts significantly the Zn to Cu ratio. Zinc concentration in low yield plants ( $0.026 \text{ mg g}^{-1}$ ) are above the critical value of zinc deficiency, i.e.  $15 \mu\text{g g}^{-1}$  (Marschner, 2012). Previously, Cu has been identified as a limiting element for fruit production due to its very low concentration in leaves (Hébert-Gentile, 2011). Copper accumulated mostly in fruit, where concentrations of  $50\text{-}65 \mu\text{g g}^{-1}$  were found (Hébert-Gentile et al., 2011). Nevertheless, Cu concentration could have reached toxic levels for cloudberry despite its overall low concentration in low yield plants, i.e.  $3 \mu\text{g g}^{-1}$ . Copper is efficiently absorbed on organic matter and on Fe oxides and hydroxides, which make it immobile in peat (Karam et al., 2003). The release of carboxylates can increase the mobility of Cu ions through its effects on Fe oxides and hydroxides (Deiana et al., 2003). Another element supporting the hypothesis that low yield plants may suffer from Cu toxicity, is their increased uptake of S which could be linked to the production of phytochelatins known to be used to detoxify Cu (Cobbett & Goldsbrough, 2002, Shahbaz et al., 2010). Phytochelatin is a metal chelator composed of cysteine, a sulfur-containing amino acid. Copper and S foliar concentration are indeed positively correlated ( $r=0.61$ ,  $P=0.0002$ ).

### **3.7 Conclusion**

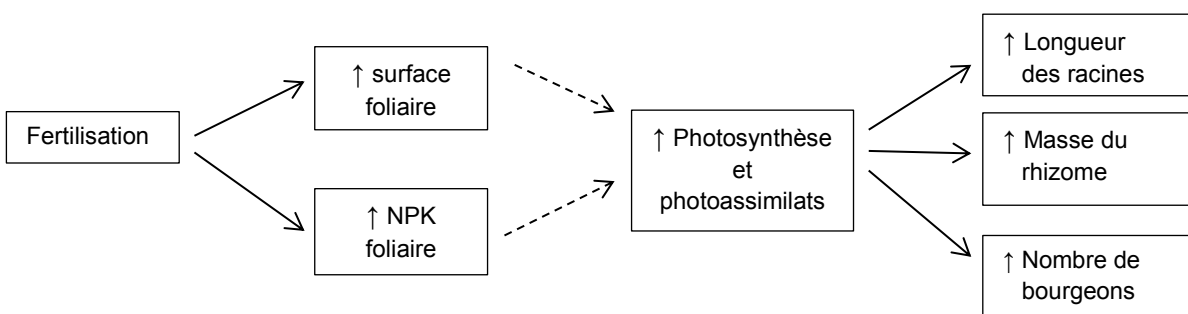
Fruit yield in New-Brunswick cloudberry populations seems to be decreasing in conditions that favour the accumulation of Mn, Fe, Cu and S in the leaves. The accumulation of Mn, Fe and Cu could be a secondary effect of an acquisition strategy aimed at either increasing P availability or at immobilizing Al in soil. However, releasing carboxylate is costly for a carbon-limited plant such as cloudberry and could explain that this strategy is associated with low yield. The accumulation of S in leaves appears to be a common phenomenon at least in Eastern Canada. Sulfur accumulation can be due to the production of phytochellatins in response to high metal concentrations.

The bimonthly leaf sampling allowed a better characterization of the seasonal change in nutrient concentration and content that takes place in leaves. Fruiting period seems the best time to sample leaves because nutrient concentrations are more stable than during flowering, whereas after fruit development is completed, leaves are already senescing.

## Chapitre 4. Conclusion générale

L'implantation de cultures de chicouté en tourbière résiduelle reste un défi de taille malgré les nouvelles connaissances acquises au cours des dernières années. La survie des boutures ainsi que la productivité des plants restent faibles et très variables. L'application de fertilisants et de différentes hormones de croissance visait à augmenter la survie et la croissance des boutures par l'augmentation de la production de racines. L'analyse des nutriments foliaires avec la méthode compositionnelle (CND) visait quant à elle à identifier les déséquilibres nutritifs liés au faible rendement en fruits de la chicouté.

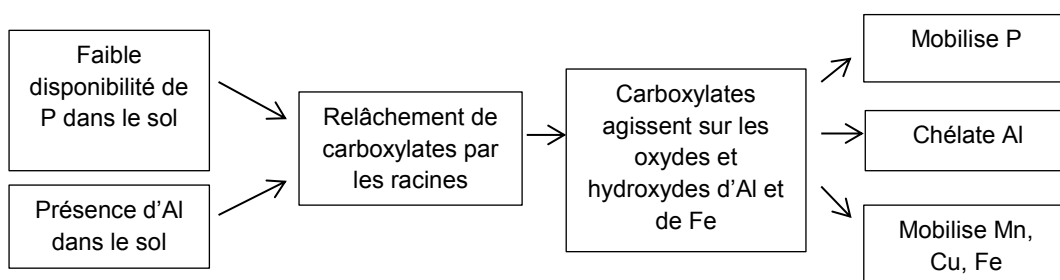
Les expériences menées dans le cadre de cette maîtrise ont permis d'améliorer la croissance suite à la plantation. Effectivement, l'expérience de fertilisation a montré l'effet positif d'un apport élevé en nutriments sur la production de racines et la croissance générale du plant (Figure 4.1). Nous espérons que cette augmentation de croissance induite par l'application de fertilisants lors de la plantation permettra un meilleur taux de survie durant les premières années de culture ainsi qu'une amélioration des taux de croissance végétative et une production de fruits plus hâtive par les boutures. Cette étude a montré que la plante produit des racines surtout à la fin de la saison, soit longtemps après l'émergence des ramets, et que la fertilisation ne permet pas un enracinement hâtif des boutures. La fertilisation n'a pas non plus permis d'augmenter les taux de survie lors de la première année. La survie des boutures semble être fortement liée aux réserves accumulées dans le rhizome à la fin de l'année précédente (Gauci et al., 2009).



**Figure 4.1** Schéma des résultats de l'expérience de fertilisation des boutures. Les lignes pleines indiquent les résultats obtenus et les lignes pointillées, des mécanismes probables pouvant expliquer ces résultats.

L'expérience sur les auxines a démontré l'effet nocif de l'application d'une auxine sur le rhizome. Malgré les faibles doses testées et le faible temps d'exposition (quelques secondes), l'application d'auxine a entraîné de très fortes mortalités. Cette mortalité est très surprenante du fait que ce phénomène n'est pas rapporté dans la littérature. L'application d'auxines semble inhiber la production de ramets sur le rhizome et la production de ramets semble être préalable à la production de racines selon l'expérience de fertilisation, ce qui peut expliquer les fortes mortalités liées au traitement d'auxine. À la lumière de ces résultats nous ne recommandons pas l'application d'auxines sur le rhizome lors de la plantation.

La récolte de feuilles au cours de la saison a permis de caractériser l'évolution des nutriments durant la saison chez la chicouté. Les concentrations foliaires de N, P, K, S, Zn et Cu diminuent au cours de la saison tandis que les concentrations de Ca, Mg, Mn, Fe augmentent durant la saison. Le diagnostic de la composition nutritive de la chicouté en tourbière naturelle a permis de cibler les balances nutritionnelles limitant la production de fruits. Les principaux nutriments impliqués dans le faible rendement sont le soufre, le manganèse, le fer et le cuivre. Ces quatre éléments sont en plus forte proportion dans les parcelles à faible rendement. L'accumulation de ces micronutriments peut refléter l'utilisation d'une stratégie de relâchement de carboxylates par les racines (figure 4.2). Les carboxylates permettent de libérer le phosphore retenu sur les oxydes et hydroxydes de fer et d'aluminium et de chélater l'aluminium ainsi libéré. Le cuivre et le manganèse peuvent aussi être libérés par ce processus. Il faut toutefois garder à l'esprit que l'analyse compositionnelle nous donne seulement des pistes sur les déséquilibres nutritionnels et que les interactions entre les nutriments compliquent l'interprétation des résultats. L'absence d'analyses de sol ne permet pas de tirer de conclusions fermes sur la cause de l'accumulation de ces micronutriments dans les feuilles.



**Figure 4.2** Schéma de la stratégie de relâchement des carboxylates et leurs effets sur la disponibilité des nutriments.

Pour que la culture de chicouté soit possible, il reste encore plusieurs points sur lesquels travailler, alors voici quelques suggestions pour de futures recherches. Puisque l'application de fertilisants et d'auxines n'a pas permis d'augmenter la survie des boutures, il faut tenter de trouver la ou les principales causes de mortalité des boutures. La survie du rhizome semble liée aux réserves carbonées accumulées l'année précédente (Gauci et al., 2009). Il faudrait donc trouver un moyen d'augmenter l'accumulation de réserves des rhizomes utilisés pour la plantation. Puisque les feuilles de chicouté ont tendance à commencer à sénescer bien avant la dégradation des conditions propices à la photosynthèse, repousser le début de la sénescence pourrait permettre d'augmenter la quantité de réserves. L'application d'hormone de croissance telle les cytokinines permet de retarder la sénescence chez la chicouté (données non-publiées). Il serait donc intéressant de tester l'application de cytokinines sur des parcelles où nous prévoyons récolter des boutures à l'automne, pour voir si cette application a un effet sur la survie des boutures et sur leurs réserves carbonées. Afin de mieux comprendre les limitations nutritionnelles identifiées dans les populations naturelles de chicouté du Nouveau-Brunswick, il serait intéressant de combiner les analyses foliaires avec des analyses de sol. Les analyses de sol permettraient de déterminer si l'accumulation de manganèse, de fer et de cuivre est liée à une plus grande disponibilité de ces nutriments dans le sol, à de plus fortes concentrations en aluminium dans certains secteurs ou à de plus faibles concentrations en phosphore.

À la suite des résultats obtenus durant cette maîtrise, nous recommandons de fertiliser lors de la plantation. L'effet de la fertilisation sur la production de fruits devra être évalué à plus long terme. Cependant, un problème majeur demeure et des approches permettant d'augmenter le taux de survie des boutures devront être développées afin d'optimiser le succès de plantation en tourbière résiduelle.

## Références

**Ågren, J. 1988a.** Between-year variation in flowering and fruit set in frost-prone and frost-sheltered populations of dioecious *Rubus chamaemorus*. *Oecologia*. 76: 175-183.

**Ågren, J. 1988b.** Sexual differences in biomass and nutrient allocation in the dioecious *Rubus chamaemorus*. *Ecology*. 69: 962-973.

**Ågren, J., Elmqvist, T., and Tunlid, A. 1986.** Pollination by deceit, floral sex ratios and seed set in dioecious *Rubus chamaemorus* L. *Oecologia*. 70: 332-338.

**Andersen, R., Rochefort, L., and Landry, J. 2011.** La chimie des tourbières du Québec: une synthèse de 30 années de données. *Nat. Can.* 135: 5-14.

**Balestri, E. and Lardicci, C. 2006.** Stimulation of root formation in *Posidonia oceanica* cuttings by application of auxins (NAA and IBA). *Mar. Biol.* 149: 393-400.

**Barnhisel, R. and P. Bertshc. 1982.** Digestion with perchloric-nitric acids. Pages 279-280 In A. L. Page, eds. *Methods of soil analysis*. Am. Soc. Agron., Madison, Wisconsin.

**Beaulieu, J., Otrysko, B., and Lapointe, L. 2001.** Note sur l'histoire naturelle de la chicouté (*Rubus chamaemorus* L.). *Nat. Can.* 125: 17-21.

**Bellemare, M. 2007.** Productivité de la chicouté au Québec en fonction de diverses régies de culture. Mémoire de Maîtrise (M. Sc. ), Département Phytologie, Université Laval, Québec, Canada. 98pp.

**Bellemare, M., Lapointe, L., Chiasson, G., Daigle, J.-Y., and Rochefort, L. 2009a.** Conditions favouring survival of cloudberry (*Rubus chamaemorus*) rhizomes planted in cutover peatland. *Mires & Peat*. 5: 1-8.

**Bellemare, M., Rochefort, L., and Lapointe, L. 2009b.** Rhizome sectioning and fertilization increase the productivity of cloudberry in natural peatlands. *Can. J. Plant. Sci.* 89: 521-526.

**Blazich, F. A. 1988a.** Chemicals and formulations used to promote adventitious rooting. Pages 132-149 In T. D. Davis, B. E. Haissing, and N. Sankhla, eds. *Adventitious root formation in cuttings*. Dioscorides Press, Portland, OR.

**Blazich, F. A. 1988b.** Mineral Nutrition and adventitious rooting. Pages 61-69 In T. D. Davis, B. E. Haissing, and N. Sankhla, eds. *Adventitious root formation in cuttings*. Dioscorides Press, Portland, OR.

**Blazich, F. A. 1988c.** Mineral nutrition and adventitious rooting. Pages 61-69 In T. D. Davis, B. E. Haissing, and N. Sankhla, eds. *Adventitious root formation in cuttings*. Dioscorides Press, Portland, OR.

**Blodau, C., Mayer, B., Peiffer, S., and Moore, T. R. 2007.** Support for an anaerobic sulfur cycle in two Canadian peatland soils. *J. Geophys. Res. Biogeosci.* 112: 1-10.

**Bolt, G. H., M. G. M. Bruggenwert, and A. Kamphorst. 1978.** Adsorption of cations by soil. Pages 54-90 In G. H. Bolt and M. G. M. Bruggenwert, eds. *Soil chemistry: A. basic elements*. Elsevier scientific publishing company, New-York, NY.

**Bould, C. 1968.** Leaf analysis as a diagnostic method and advisory aid in crop nutrition. *Expl. Agric.* 4: 17-27.



- Brix, H. and Lyngby, J. E. 1985.** Uptake and translocation of phosphorus in eelgrass (*Zostera marina*). *Mar. Biol.* 90: 111-116.
- Brooker, R. W., Callaghan, T. V., and Jonasson, S. 1999.** Nitrogen uptake by rhizomes of the clonal sedge *Carex bigelowii*: a previously overlooked nutritional benefit of rhizomatous growth. *New Phytol.* 142: 35-48.
- Brown, A. O. and McNeil, J. N. 2009.** Pollination ecology of the high latitude, dioecious cloudberry (*Rubus chamaemorus*; Rosaceae). *Am. J. Bot.* 96: 1096-1107.
- Bussi eres, J., Rochefort, L., and Lapointe, L. 2015.** Cloudberry cultivation in cutover peatland: Improved growth on less decomposed peat. *Can. J. Plant. Sci.* 95: 479-489.
- Campbell, D. R. and L. Rochefort. 2001.** La v eg etation: gradients. Pages 129-140 In S. Payette and L. Rochefort, eds. * cologie des tourbi eres du Qu ebec-Labrador*. Presses Universit  Laval, Qu ebec, Canada.
- Centre d'expertise sur les produits forestiers. 2008.** Mise en valeur des produits forestiers non ligneux. [Online] Available: [http://www.bioperre.com/medias/public/ldv\\_4bacea1e03ac7\\_Etude\\_de\\_marche\\_sur\\_les\\_PFNL\\_-\\_mise\\_en\\_valeur\\_DEC.pdf](http://www.bioperre.com/medias/public/ldv_4bacea1e03ac7_Etude_de_marche_sur_les_PFNL_-_mise_en_valeur_DEC.pdf) [20160 Apr. 15].
- Chapin, F. S. III. 1980.** The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11: 233-260.
- Cobbett, C. and Goldsbrough, P. 2002.** Phytochelatins and metallothioneins: Roles in heavy metal detoxification and homeostasis. *Annu. Rev. Plant Biol.* 53: 159-182.
- Costal, J. M., Heuvelink, E., Van de Pol, P. A., and Put, H. M. C. 2007.** Anatomy and morphology of rooting in leafy rose stem cuttings and starch dynamics following severance. *Acta Hort.* 751: 495-502.
- Coutts, M. P. and Philipson, J. J. 1977.** Influence of mineral-nutrition on root development of trees .3. Plasticity of root-growth in response to changes in nutrient environment. *J. Exp. Bot.* 28: 1071-1075.
- Damman, A. W. H. 1978.** Distribution and movement of elements in ombrotrophic peat bogs. *Oikos.* 30: 480-495.
- Damman, A. W. H. 1986.** Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. *Can. J. Bot.* 64: 384-394.
- Davis, T. D. 1988.** Photosynthesis during adventitious rooting. Pages 79-87 In T. D. Davis, B. E. Haissig, and N. Sankhla, eds. *Adventitious root formation in cuttings*. Dioscorides press, Portland, OR.
- Deiana, S., Gessa, C., Palma, A., Premoli, A., and Senette, C. 2003.** Influence of organic acids exuded by plants on the interaction of copper with the polysaccharidic components of the root mucilages. *Org. Geochem.* 34: 651-660.
- Dominguez, N., Garcia-Escudero, E., Romero, I., Benito, A., and Martin, I. 2015.** Leaf blade and petiole nutritional evolution and variability throughout the crop season for *Vitis vinifera* L. cv. Graciano. *Span. J. Agric. Res.* 13: 1-17.
- Dumas, P. and Maillette, L. 1987.** Rapport des sexes, effort et succ s de reproduction chez *Rubus chamaemorus*, plante herbac e vivace dioique de distribution subarctique. *Can. J. Bot.* 65: 2628-2639.

**Environnement Canada. 2015.** Climate normals and averages. [Online] Available: [http://climat.meteo.gc.ca/index\\_f.html](http://climat.meteo.gc.ca/index_f.html) [2016 Apr. 10].

**Epstein, E. and A. J. Bloom. 2005.** Mineral nutrition of plants: Principles and perspectives. Sinauer Associates, Incorporated, Sunderland, MA

**Evans, J. R. 1989.** Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia*. 78: 9-19.

**Fageria, N. K. and A. Moreira. 2011.** The role of mineral nutrition on root growth of crop plants. Pages 251-331 In L. S. Donald, eds. *Advances in agronomy*. Elsevier Academic Press Inc, San Diego, CA.

**Fernandez, M. C. and Rubio, G. 2015.** Root morphological traits related to phosphorus-uptake efficiency of soybean, sunflower, and maize. *J. Plant Nutr. Soil Sc.* 178: 807-815.

**Gauci, R. 2008.** Étude de certains facteurs influençant la production de fruits et de ramets floraux chez la chicouté (*Rubus chamaemorus*). PhD Thesis, Université Laval, Québec, Canada. 146pp.

**Gauci, R., Otrysko, B., Catford, J. G., and Lapointe, L. 2009.** Carbon allocation during fruiting in *Rubus chamaemorus*. *Ann. Bot.* 104: 703-713.

**Ghannoum, O. and Conroy, J. P. 2007.** Phosphorus deficiency inhibits growth in parallel with photosynthesis in a C<sub>3</sub> (*Panicum laxum*) but not two C<sub>4</sub> (*P. coloratum* and *Cenchrus ciliaris*) grasses. *Funct. Plant Biol.* 34: 72-81.

**Gjengedal, E. 1996.** Effects of soil acidification on foliar leaching and retranslocation of metals in vascular plants. *Water Air Soil Poll.* 86: 221-234.

**Grigal, D. F., Ohmann, L. F., and Brander, R. B. 1976.** Seasonal dynamics of tall shrubs in Northeastern Minnesota - Biomass and nutrient element changes. *Forest Sci.* 22: 195-208.

**Groupe de recherche en écologie des tourbières. 2009.** Production de petits fruits en tourbières, 2<sup>e</sup> ed. Université Laval, Québec, QC. 132p.

**Guha, M. M. and Mitchell, R. L. 1966.** Trace and major element composition of leaves of some deciduous trees. II. Seasonal changes. *Plant & Soil.* 24: 90-112.

**Hartmann, T. H., D. E. Kester, Jr. F. T. Davies, and R. L. Geneve. 2011.** Plant propagation: Principles and practices, 8<sup>th</sup> ed. Prentice-Hall, Upper Saddle River, N.J. 770p.

**Hayes, P., Turner, B. L., Lambers, H., and Laliberte, E. 2014.** Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. *J. Ecol.* 102: 396-410.

**Hébert-Gentile, V. 2011.** Fertilisation biologique en tourbière naturelle et application foliaire du bore et de cuivre chez la chicouté. Mémoire De Maîtrise (M. Sc. ), Département Phytologie, Université Laval, Québec, Canada. 83pp.

**Hébert-Gentile, V., Naess, S. K., Parent, L. E., and Lapointe, L. 2011.** Organo-mineral fertilization in natural peatlands of the Quebec North-Shore, Canada: Dispersion in soil and effects on cloudberry growth and fruit yield. *Acta Agri. Scand. Sect. B-Soil Plant Sci.* 61: 8-17.

- Ikeuchi, M., Sugimoto, K., and Iwase, A. 2013.** Plant callus: Mechanisms of induction and repression. *Plant Cell*. 25: 3159-3173.
- Jaakkola, M., Korpelainen, V., Hoppula, K., and Virtanen, V. 2012.** Chemical composition of ripe fruits of *Rubus chamaemorus* L. grown in different habitats. *J. Sci. Food and Agric.* 92: 1324-1330.
- Jean, D. and Lapointe, L. 2001.** Limited carbohydrate availability as a potential cause of fruit abortion in *Rubus chamaemorus*. *Physiol. Plant.* 112: 379-387.
- Karam, A., C. Côté, and L.-É. Parent. 2003.** Retention of copper in Cu-enriched organics soils. Pages 137-150 In L.-É. Parent and P. Ilnicki, eds. *Organics soils and peat materials for sustainable agriculture*. CRC Press, Boca Raton, FL.
- Karst, A. L. and Turner, A. J. 2011.** Local ecological knowledge and importance of bakeapple (*Rubus chamaemorus*) in a southeast Labrador métis community. *Ethnobiology Letters*. 2: 6-18.
- Korpelainen, H. 1994.** Sex ratios and resource allocation among sexually reproducing plants of *Rubus chamaemorus*. *Ann. Bot.* 74: 627-632.
- Kortesharju, J. 1988.** Cloudberry yields and factors affecting the yield in Northern Finland. *Acta. Bot. Fenn.* 136: 77-80.
- Kortesharju, J. and Rantala, E. M. 1980.** The effect of placement fertilization on cloudberry (*Rubus chamaemorus* L.) on unditched bog. *Suo*. 31: 85-92.
- Lambers, H., Hayes, P. E., Laliberte, E., Oliveira, R. S., and Turner, B. L. 2015.** Leaf manganese accumulation and phosphorus-acquisition efficiency. *Trends Plant Sci.* 20: 83-90.
- Lambers, H., J. Stulen, and J. Neeteson. 1985.** Fundamental, ecological and agricultural aspects of nitrogen metabolism in higher plants: Proceedings of a symposium organized by the Department of Plant Physiology, University of Groningen and the Institute for Soil Fertility, Haren, BEL
- Leopold, A. C. 1963.** The occurrence and role of growth hormones in plants. Pages 60-93 In A. C. Leopold, eds. *Auxins and plant growth*. University of California Press, Berkeley and Los Angeles, CA.
- Liu, H. S., Liu, H. J., and Song, Y. H. 2011.** Absorption and translocation of nitrogen in rhizomes of *Leymus chinensis*. *Rapid Commun. Mass Spectrom.* 25: 665-671.
- Lloyd, D. G. 1974.** Theoretical sex-ratios of dioecious and gynodioecious angiosperms. *Heredity*. 32: 11-34.
- Lynch, J. P. and Ho, M. D. 2005.** Rhizoeconomics: Carbon costs of phosphorus acquisition. *Plant Soil*. 269: 45-56.
- Mäkinen, Y. and Oikarinen, H. 1974.** Cultivation of cloudberry in Fennoscandia. *Rep. Kevo Subarct. Res. Stn.* 11: 90-102.
- Marie-Victorin, F., L. Brouillet, E. Rouleau, I. Goulet, and S. Hay. 2002.** *Flore Laurentienne*, 3rd ed. Gaëtan Morin éditeur Ltée, Boucherville, QC. 1093p.
- Marschner, H. 2012.** *Mineral nutrition of higher plants*. 3e ed. Academic Press, London, UK. 889p.

- Martin, N. M. and Maricle, B. R. 2015.** Species-specific enzymatic tolerance of sulfide toxicity in plant roots. *Plant Physiol. Bioch.* 88: 36-41.
- Martinussen, I., Nilsen, G., Svenson, L., Junttila, O., and Rapp, K. 2004.** In vitro propagation of cloudberry (*Rubus chamaemorus*). *Plant Cell Tissue Organ Cult.* 78: 43-49.
- Mehlich, A. 1984.** Mehlich 3 soil test extractant: A modification of Mehlich 2 extractant. *Commun. Soil Sci. Plant Anal.* 15: 1409-1416.
- Mengel, K. and E. A. Kirkby. 1978.** Phosphorus. Pages 347-366 In K. Mengel and E. A. Kirkby, eds. *Principles of plant nutrition.* International Potash Institute, Worblaufen-Bern, Switzerland.
- Millar, C. E. and L. M. Turk. 1943.** Physical and chemical properties of soils. Pages 67-93 In C. E. Millar and L. M. Turk, eds. *Fundamentals of soil science.* Wiley, New-York, NY.
- Ministère de l'énergie et des mines. 2010.** Politique sur l'extraction de la tourbe. Gouvernement du Nouveau-Brunswick. 15p.
- Ministère de l'énergie et des mines. 2015.** Information sur l'industrie de la tourbe 2014p. Gouvernement du Nouveau-Brunswick. 3p.
- Mokany, K. and Ash, J. L. 2008.** Are traits measured on pot grown plants representative of those in natural communities? *J. Veg. Sci.* 19: 119-126.
- Moreira, A. and Fageria, N. K. 2009.** Yield, uptake, and retranslocation of nutrients in banana plants cultivated in upland soil of central Amazonian. *J. Plant Nutr.* 32: 443-457.
- Nilsen, G. S. 2005.** Cloudberry- The northern gold. *Int. J. Fruit Sci.* 5: 45-60.
- Nocito, F. F., Lancilli, C., Crema, B., Fourcroy, P., Davidian, J. C., and Sacchi, G. A. 2006.** Heavy metal stress and sulfate uptake in maize roots. *Plant Physiol.* 141: 1138-1148.
- Oliveira, R. S., Galvao, H. C., de Campos, M. C. R., Eller, C. B., Pearse, S. J., and Lambers, H. 2015.** Mineral nutrition of campos rupestres plant species on contrasting nutrient-impooverished soil types. *New. Phytol.* 205: 1183-1194.
- Østgård, O. 1964.** Investigations on cloudberry (*Rubus chamaemorus* L.) in North- Norway. *Forsk. Fors. Landbr.* 15: 409-444.
- Parent, L.-É., Parent, S.-É., Hébert-Gentile, V., Naess, S. K., and Lapointe, L. 2013.** Mineral balance plasticity of cloudberry (*Rubus chamaemorus*) in Quebec-Labrador bogs. *Am. J. Plant Sci.* 4: 1508-1520.
- Parent, L.-É., Parent, S.-É., Rozane, D. E., Amorim, D. A., Hernandes, A., and Natale, W. 2012.** Unbiased approach to diagnose the nutrient status of red guava (*Psidium guajava*). *Acta Hort.* 959: 145-159.
- Payette, S. 2015.** Flore nordique du Québec Labrador, tome 2. Presses de l'Université Laval, Québec, Canada, 711 p.
- Payette, S. and L. Rochefort. 2001.** Écologie des tourbières. Les Presses de l'Université Laval, Québec, QC. 621p.

**Pop, T. I., Pamfil, D., and Bellini, C. 2011.** Auxin control in the formation of adventitious roots. *Not. Bot. Horti. Agrobo.* 39: 307-316.

**Rabenhorst, M. C. and D. Swanson. 2000.** Histosols. Page E183-E209 In M. Summer, ed. *Handbook of soil science*. CRC Press, Boca Raton, FL.

**Rapp, K. 2004.** *Cloudberry growers guide*. North Norwegian Centre for Research and Rural Development, Tromsø, Norway. 15p.

**Rapp, K. and Steenberg, K. 1977.** Studies of phosphorus uptake from different depths in cloudberry mires using <sup>32</sup>P-labelled fertilizer. *Acta. Agri. Scand.* 27: 319-325.

**Raven, P. H., S. E. Eichhorn, and R. F. Evert. 2014.** *Biologie végétale*, 3 ed. De Boeck, New-York, NY. 944p.

**Resvoll, T. R. 1929.** *Rubus chamaemorus* L. : a morphological-biological study. *Nyt Mag. F. Naturvidensk.* 67: 55-129.

**Robinson, D. 1990.** Phosphorus availability and cortical senescence in cereal roots. *J. Theor. Biol.* 145: 257-265.

**Rydin, H. and J. K. Jeglum. 2013.** *The biology of peatlands*. Oxford University Press, Oxford, UK. 354p.

**Saastamoinen, O. 1998.** Non-wood goods and benefits of boreal forests: concepts and issues. Pages 47-57 In H. G. Lund, B. Pajari, and M. Korhonen, eds. *Sustainable development of non-wood goods and benefits from boreal and cold temperate forests*. European Forest Institute, Joensuu, Finland.

**Saastamoinen, O., Kangas, K., and Aho, H. 2000a.** The picking of wild berries in Finland in 1997 and 1998. *Scand. J. For. Res.* 15: 645-650.

**Saastamoinen, O., Kangas, K., and Aho, H. 2000b.** The picking of wild berries in Finland in 1997 and 1998. *Scand. J. For. Res.* 15: 645-650.

**Santos, K. M., Fisher, P. R., Yeager, T. H., Simonne, E. H., Carter, H. S., and Argo, W. R. 2011.** Effect of *Petunia* stock plant nutritional status on fertilizer response during propagation. *J. Plant Nutr.* 34: 1424-1436.

**Schwambach, J., Fadanelli, C., and Fett-Neto, A. G. 2005.** Mineral nutrition and adventitious rooting in microcuttings of *Eucalyptus globulus*. *Tree Physiol.* 25: 487-494.

**Shahbaz, M., Tseng, M. H., Stuiver, C. E. E., Koralewska, A., Posthumus, F. S., Venema, J. H., Parmar, S., Schat, H., Hawkesford, M. J., and De Kok, L. J. 2010.** Copper exposure interferes with the regulation of the uptake, distribution and metabolism of sulfate in Chinese cabbage. *J. Plant Physiol.* 167: 438-446.

**Small, E. and Catling, P. M. 2000.** Poorly known economic plants of Canada - 27. *Cloudberry, Rubus chamaemorus*. *CBA Bull.* 33: 43-47.

**Srivastava, L. M. 2002.** *Plant growth and development: Hormones and environment*. Academic Press, San Diego, CA. 772p.

**Taylor, K. 1971.** Biological Flora of British-Isles - *Rubus chamaemorus* L. *J. Ecol.* 59: 293-306.

**Théroux-Rancourt, G., Rochefort, L., and Lapointe, L. 2009.** Cloudberry cultivation in cutover peatlands: hydrological and soil physical impacts on the growth of different clones and cultivars. *Mires & Peat.* 5: 1-16.

- Thiem, B. 2001.** Micropropagation of Cloudberry (*Rubus chamaemorus* L.) by initiation of axillary shoots. Acta Soc. Bot. Pol. 70: 11-16.
- Topp, G. C. and Zebchuk, W. 1979.** Determination of soil-water desorption curves for soil cores. Can. J. Soil Sci. 59: 19-26.
- Tyson, M. J., Oughton, D. H., Callaghan, T. V., Day, J. P., and Sheffield, E. 1990.** The uptake and translocation of <sup>134</sup>Caesium and <sup>85</sup>Strontium in bracken *Pteridium aquilinum* (Dennstaedtiaceae:Pteridophyta). Fern Gaz. 13: 381-383.
- Viers, J., Prokushkin, A. S., Pokrovsky, O. S., Auda, Y., Kirilyanov, A. V., Beaulieu, E., Zouiten, C., Oliva, P., and Dupre, B. 2013.** Seasonal and spatial variability of elemental concentrations in boreal forest larch foliage of Central Siberia on continuous permafrost. Biogeochemistry. 113: 435-449.
- Wang, B. L., Shen, J. B., Zhang, W. H., Zhang, F. S., and Neumann, G. 2007.** Citrate exudation from white lupin induced by phosphorus deficiency differs from that induced by aluminum. New. Phytol. 176: 581-589.
- Wang, Y. L., Almvik, M., Clarke, N., Eich-Greatorex, S., Ogaard, A. F., Krogstad, T., Lambers, H., and Clarke, J. L. 2015.** Contrasting responses of root morphology and root-exuded organic acids to low phosphorus availability in three important food crops with divergent root traits. AOB Plants. 7: 1-11.
- Wesley, P. H. 1988.** Donor plant maturation and adventitious root formation. Pages 11-28 In T. D. Davis, B. E. Haissig, and N. Sankhla, eds. Adventitious root formation in cuttings. Dioscorides Press, Portland, OR.

# Annexes

**Annexe 1** : Caractéristiques chimiques et physiques de la tourbe dans les parcelles de fertilisation (chapitre 2).

Table A1. Caractéristiques de la tourbe selon les traitements de l'expérience fertilisation. Moyenne (erreur-type).  $N=3$

Traitements	pH	M.O (%)	BD ( $\text{g cm}^{-3}$ )
Témoin	3.13 (0.007)	94.7 (0.7)	0.097 (0.011)
100-100-100	3.15 (0.01)	96.5 (1.5)	0.104 (0.007)
50-100-100	3.14 (0.02)	93.4 (0.7)	0.110 (0.014)
50-100-50	3.15 (0.02)	97.7 (1.1)	0.110 (0.014)

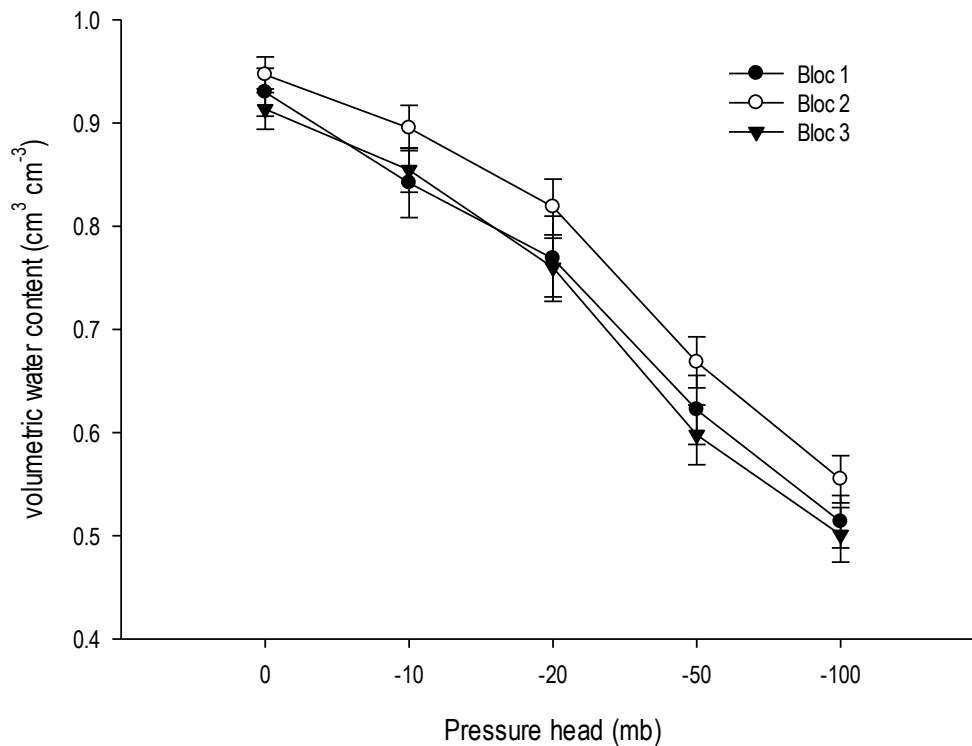


Figure A1. Courbe de rétention de l'eau par les échantillons de tourbe par bloc selon les pressions appliquées sur l'échantillon. Moyenne  $\pm$  erreur-type.  $N=4$

**Annexe 2.** Localisation des parcelles en tourbières naturelles du chapitre 3.

Table A2. Coordonnées GPS de chaque tourbière naturelle utilisée en 2013 et 2014 avec les codes utilisés lors de la saisie de données.

Année	Tourbière	Coordonnées GPS	Code
2013	1	N 47 44.409 W064 44.695	HS
2013	2	N 47 45.783 W064 40.539	Lam
2013	3	N 47 43.182 W064 41.063	PS
2013	4	N 47 43.612 W064 43.685	Tom
2014	5	N 47 49.072 W064 33.317	MA
2014	6	N 47 50.566 W064 32.588	PG
2014	7	N 47 41.496 W064 45.715	CAT
2014	8	N 47 40.321 W064 45.808	SG
2014	2 (année 2)	N 47 45.673 W064 40.665	Lam

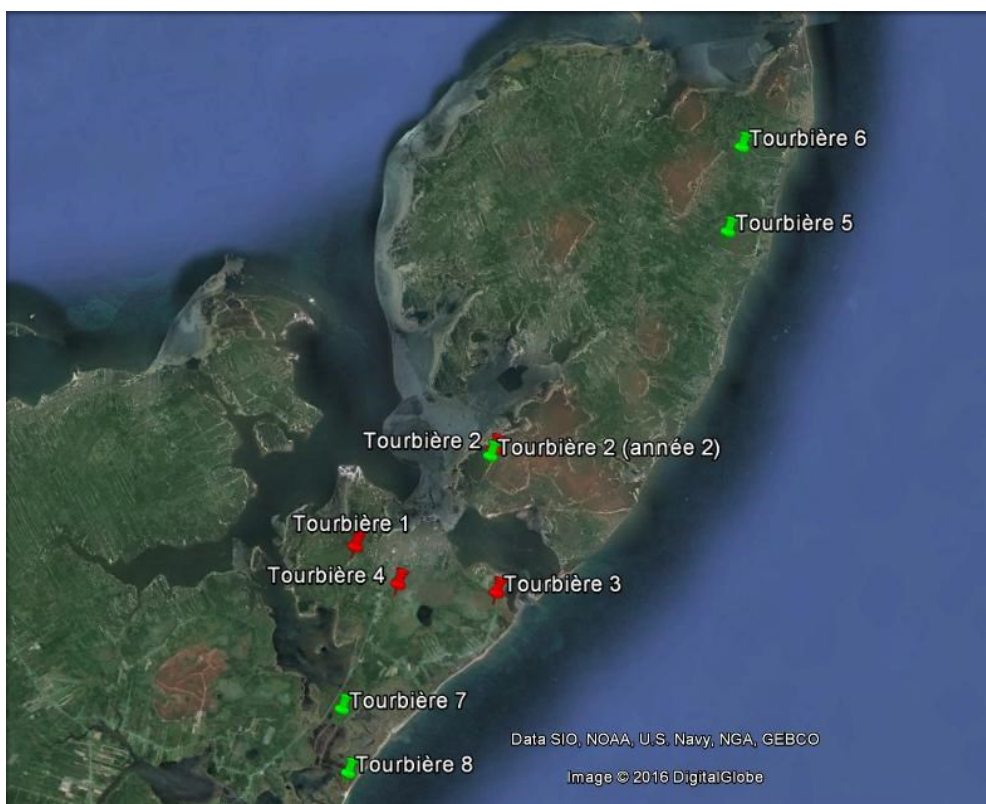


Figure A2. Carte des tourbières naturelles visitées dans le cadre du chapitre 3. Les points rouges sont les tourbières visitées en 2013 et les points verts sont les tourbières visitées en 2014.



### Annexe 3. Partition binaire séquentielle des balances nutritionnelles

Table A3. Partition binaire séquentielle des balances nutritionnelles utilisées dans l'analyse compositionnelle. Les +1 représentent les éléments au dénominateur dans les balances et les -1 représentent les éléments au numérateur dans le calcul des *ilrs*.

définition <i>ilr</i>	Fv	C	P	K	Mg	Ca	S	N	Al	Mn	Fe	Zn	Cu
Fv C,P,K,Mg,Ca,S,N,Al,Mn,Fe,Zn,Cu	-1	1	1	1	1	1	1	1	1	1	1	1	1
C P,K,Mg,Ca,S,N,Al,Fe,Mn,Zn,Cu	0	-1	1	1	1	1	1	1	1	1	1	1	1
P,K,Mg,Ca,S,N Al,Mn,Fe,Zn,Cu	0	0	-1	-1	-1	-1	-1	-1	1	1	1	1	1
P,K,Mg,Ca S,N	0	0	-1	-1	-1	-1	1	1	0	0	0	0	0
P,K Mg,Ca	0	0	-1	-1	1	1	0	0	0	0	0	0	0
Mg Ca	0	0	0	0	-1	1	0	0	0	0	0	0	0
P K	0	0	-1	1	0	0	0	0	0	0	0	0	0
S N	0	0	0	0	0	0	-1	1	0	0	0	0	0
Al,Mn,Fe Zn,Cu	0	0	0	0	0	0	0	0	-1	-1	-1	1	1
Al Mn,Fe	0	0	0	0	0	0	0	0	-1	1	1	0	0
Fe Mn	0	0	0	0	0	0	0	0	0	1	-1	0	0
Zn Cu	0	0	0	0	0	0	0	0	0	0	0	-1	1