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**LES EFFETS FERTILISANTS DE LA GRANDE OIE
DES NEIGES SUR LA DYNAMIQUE DES MILIEUX
HUMIDES DE L'ÎLE BYLOT AU NUNAVUT :
IMPACT DU TAPIS DE BRYOPHYTES**

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Résumé

La productivité, la décomposition et le recyclage des nutriments sont faibles dans les polygones de tourbe de l'île Bylot. La présence de la Grande oie des neiges pourrait y modifier ces paramètres, car ses fèces contiennent des nutriments facilement assimilables. Il faut cependant considérer l'abondance des mousses. Le rôle important des mousses dans la dynamique des milieux humides a été confirmé par cette étude. À court terme, elles séquestrent les nutriments ajoutés par les fèces. Les plantes broutées ont accès aux nutriments uniquement lorsque les mousses sont saturées et que les nutriments atteignent leurs racines. La décomposition et le recyclage des nutriments ne sont pas affectés. Il semble donc qu'à court terme, l'effet fertilisant de l'oie n'est visible que sur la croissance des mousses. En résultat secondaire, cette étude a démontré que la technique des marqueurs naturels est la plus appropriée pour estimer la production primaire des mousses dans les milieux humides arctiques.

Abstract

Productivities, decomposition rates and nutrient turnovers are low in polygon fens of Bylot Island. The Greater snow geese population could modify these parameters since goose faeces contain nutrients that are easily uptaken. However, it is important to consider the moss carpet. This study showed that mosses play an important role on the polygon fen dynamic by sequestering the nutrients added by goose faeces. Grazed plants were able to uptake nutrients only when the mosses are saturated and consequently, when nutrients reach their roots. The decomposition rates and the turnover of nutrients were not affected by nutrient additions. In addition, in the short-term, it seems that fertilizing effect of geese was visible only on moss growth. As a secondary result, this study showed that innate marker method is the most appropriate to estimate moss primary production in arctic wetlands.

Avant-propos

J'ai rédigé les premier et deuxième chapitres sous forme d'article. Line Rochefort, directrice et Gilles Gauthier, co-directeur et co-auteurs les ont révisés pour publication. Chantal Pineau est une des auteurs du premier article car une partie des données proviennent de son travail de maîtrise et mon mémoire est une suite logique de son travail.

Pour le premier chapitre, les données du premier essai de fertilisation ("FTF experiment") ont été prises durant la maîtrise de Chantal Pineau par ses assistants et elle-même. Par contre, j'ai refait toutes les analyses statistiques, les figures, les tableaux et la discussion ayant rapport à cet essai. Les données du deuxième essai de fertilisation ("STF experiment") proviennent de mon travail de maîtrise. Mes assistants et moi-même avons pris toutes les données reliées à cet essai. J'ai également fait toutes les analyses, les figures et les tableaux pour cet essai.

Pour le deuxième chapitre, les données de l'expérience sur les tiges coudées et les marqueurs naturels ("CW-I experiment") ont été prises par Chantal Pineau et ses assistants. Les données de l'expérience sur les marqueurs permanents blancs et les marqueurs naturels ("WM-I experiment") ont été prises dans le cadre de ma maîtrise par mes assistants et moi-même. J'ai traité les données des deux expériences, j'ai fait toutes les analyses, les figures et les tableaux et l'idée de comparer différentes méthodes d'estimation de production des mousses est une idée originale de ce mémoire.

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Introduction générale

1.0 Introduction

Les milieux humides arctiques subissent des pressions climatiques très importantes. Il arrive aussi fréquemment que des populations importantes d'herbivores utilisent ces habitats pour leur quête alimentaire. De plus, les liens trophiques entre les plantes et les herbivores sont à la base des interactions présentes dans plusieurs de ces écosystèmes de toundra. La présence d'un broutement modéré par des oies dans certains sites sub-arctiques au Canada s'est avéré favorable au fonctionnement de l'écosystème en stimulant la croissance des plantes. Cependant, ce n'est pas le cas à l'île Bylot, où une population de Grande oie des neiges se nourrit dans les polygones de tourbe pendant la période estivale. Et ce, même si leurs fèces contiennent des grandes quantités de nutriments solubles et facilement assimilables, ce qui peut potentiellement accélérer le cycle des nutriments. Les mousses sont également très abondantes dans les milieux humides de l'île Bylot et elles ne sont généralement pas broutées. Nous soupçonnons que les mousses séquestrent les nutriments provenant des fèces, empêchant ainsi les plantes graminoides d'en profiter. Une attention particulière a donc été portée sur le rôle potentiel de la strate muscinale au niveau des interactions trophiques présentes dans cet écosystème. Cette étude devrait aider à comprendre les effets à court terme de l'ajout de nutriments via les fèces d'oies sur la dynamique de la végétation des milieux humides arctiques.

1.1 Caractéristiques des milieux arctiques

La production primaire annuelle des écosystèmes des régions arctiques est beaucoup plus faible que celle des écosystèmes des régions tempérées (Haag 1974). Une saison de croissance courte, des précipitations peu abondantes et une disponibilité restreinte en éléments nutritifs sont autant de facteurs qui expliquent pourquoi la production primaire de ces milieux est si faible (Haag 1974; Chapin et Shaver 1985). De plus, les plantes ne reçoivent qu'une faible partie des rayons du soleil, car l'angle avec lequel ils frappent le sol fait en sorte que les processus de réflexion et de réfraction sont très importants. La faible production primaire des milieux arctiques s'explique également par des processus de décomposition qui sont considérablement ralentis. Puisque la décomposition régule en

partie le recyclage des éléments nutritifs, ceux-ci redeviennent disponibles pour les plantes arctiques à un rythme très lent. En effet, la faible disponibilité en éléments nutritifs est expliquée en grande partie par les températures peu élevées du sol qui inhibent l'activité microbienne (Henry et Jefferies 2003a), laquelle est pourtant essentielle à la décomposition et au recyclage des éléments nutritifs. La majeure partie des éléments nutritifs se trouve donc immobilisée dans la matière organique qui se décompose très progressivement (Shaver *et al.* 1992).

Les plantes se sont adaptées aux faibles concentrations en nutriments de ces écosystèmes en augmentant leur biomasse racinaire (Shaver et Cutler 1979), en développant une grande capacité d'absorption à basse température (Chapin *et al.* 1978), en ayant un bon potentiel d'association avec des mycorhizes (i.e. possédant beaucoup de réserves en hydrates de carbone; Chapin *et al.* 1986) et en étant capables de réabsorber efficacement les nutriments de leurs parties sénescentes (Jonasson et Shaver 1999). Les plantes vasculaires peuvent elles-mêmes influencer la concentration en nutriments dans les sols arctiques. Dans les milieux où les concentrations en éléments nutritifs sont faibles, les plantes ont de faibles taux de croissance et elles utilisent les nutriments efficacement. Ce qui fait en sorte qu'elles produisent une litière contenant peu de nutriments qui se décompose lentement. Les plantes influencent ainsi directement le cycle des nutriments par les processus d'assimilation et d'absorption ou via les bris cellulaires et indirectement en influençant l'activité microbienne et l'herbivorisme (Hobbie 1992).

Les mousses sont très abondantes dans les écosystèmes arctiques et peuvent même par endroit représenter la totalité des espèces présentes (Russell 1990). Elles contiennent de nombreuses substances peu décomposables (phénols, hémicelluloses, fibres) (Johnson et Damman 1993) et contribuent ainsi aux faibles taux de décomposition dans les milieux arctiques. À cause de leur physiologie unique et de leur écologie, les bryophytes diffèrent des plantes vasculaires dans leur influence sur le cycle des nutriments. Les mousses sont poïkilohydriques, c'est-à-dire qu'elles absorbent l'eau sur toute leur surface et elles sont très résistantes à la dessiccation. Elles peuvent aussi acquérir leurs nutriments sur leur surface en entier et la structure particulière de leur membrane cellulaire (cuticule peu développée) facilite les échanges de solutions, de gaz et d'ions directement avec

l'environnement (Brown et Bates 1990). Elles ont ainsi une capacité d'échange ionique plus élevée que les plantes vasculaires (Clymo 1963; Craigie et Maass 1966). Les bryophytes sont donc des puits importants de nutriments (Turetsky 2003).

Les mousses sont aussi très efficaces dans la compétition avec les plantes vasculaires pour les nutriments. La capacité qu'ont les mousses à séquestrer les nutriments provoque souvent une exclusion compétitive de plusieurs espèces de plantes vasculaires (Malmer *et al.* 2003). Par contre, il existe également une forte relation négative entre le couvert et la richesse des plantes vasculaires et la biomasse des bryophytes (Virtanen *et al.* 2000; Heijmans *et al.* 2001). Lorsque la biomasse des plantes vasculaires augmente, la croissance des mousses est négativement affectée. Ceci est surtout causé par la diminution de la luminosité. En effet, la croissance des mousses est optimisée sous une combinaison de radiation et d'humidité particulière (Bergamini *et al.* 2001). L'augmentation de la biomasse des plantes vasculaires change donc cette combinaison optimale en rendant le milieu plus sec (augmentation de l'évapotranspiration) et moins ensoleillé. Les mousses jouent finalement un rôle vital dans les écosystèmes arctiques. Elles stabilisent le sol, préviennent l'érosion, maintiennent l'humidité du sol, ont des propriétés isolantes, interceptent les polluants et augmentent la fixation de l'azote (Press *et al.* 1998).

La croissance des plantes vasculaires des milieux arctiques semble être d'abord limitée par l'azote (Mckendrick *et al.* 1978; Cargill et Jefferies 1984a; Shaver et Chapin 1995), alors que la croissance des bryophytes ne semble pas l'être (Pineau 1999). Les plantes arctiques, vasculaires ou non, peuvent assimiler directement l'azote sous forme d'ions NH_4^+ et NO_3^- , ainsi que sous forme d'acides aminés (Chapin *et al.* 1993; Kielland 1994; Atkin 1996; Henry et Jefferies 2003b). La forme NH_4^+ serait la plus abondante dans les milieux humides arctiques puisque les faibles températures inhibent davantage la nitrification (NH_4^+ vers NO_3^-) que l'ammonification (azote protéique vers NH_4^+) et puisque le NO_3^- est lessivé plus rapidement (Koch *et al.* 1991). Ces sols contiennent aussi des concentrations importantes d'acides aminés libres (Atkin 1996; Henry et Jefferies 2002). Les plantes peuvent court-circuiter l'étape de la minéralisation, qui est limitée par les faibles températures, en absorbant des acides aminés directement du sol, ce qui accélère le recyclage des nutriments (Chapin *et al.* 1993; Kielland 1994). L'absorption d'azote

organique semble être une adaptation fréquente des plantes arctiques à la faible productivité du milieu. Les acides aminés pourraient constituer jusqu'à la moitié de l'azote absorbé par les plantes des milieux arctiques (Kielland 1997). Les taux d'absorption des acides aminés sont directement proportionnels à leur poids moléculaire (Kielland 1994). La glycine, l'acide aminé ayant le plus petit poids moléculaire, a le plus grand potentiel d'absorption (Chapin *et al.* 1993).

Bien qu'il soit rarement limitant, les plantes doivent avoir accès à des quantités suffisantes de phosphore pour croître lorsque l'azote est disponible à des concentrations adéquates (Gordon *et al.* 2001). Néanmoins, dans certains cas, le phosphore peut s'avérer limitant pour la croissance des plantes vasculaires et des bryophytes en milieux arctiques (Haag 1974, Gordon *et al.* 2001), principalement parce que la majorité du phosphore est immobilisée rapidement (lié à des métaux) et est ainsi difficilement absorbable. Les plantes assimilent le phosphore sous ses formes inorganiques (PO_4^{3-} , HPO_4^{2-} et H_2PO_4^-), provenant principalement de la décomposition de la matière organique, mais aussi des précipitations et de l'érosion (Chapin *et al.* 1978). Le cycle du phosphore dans les milieux arctiques est surtout régulé par les propriétés des sols, comme le pH ou l'humidité (Kielland et Chapin 1994). Par exemple, il y aura davantage de phosphore disponible lors des périodes plus sèches qui entraînent une baisse de la nappe phréatique, puisque la décomposition sera favorisée (Dirk *et al.* 1999).

La disponibilité de l'azote et du phosphore pour la végétation est régulée par les apports provenant des précipitations et du ruissellement, mais surtout par la minéralisation de la matière organique (Verhoeven 1986). Puisque ce processus est le résultat de l'activité microbienne, il importe d'examiner la relation entre les plantes et les micro-organismes dans les cycles des éléments nutritifs. Dans les environnements arctiques, les plantes et les micro-organismes sont mutuellement limités par l'un ou l'autre des éléments nutritifs. Selon Kaye et Hart (1997), les micro-organismes sont, à court terme, de meilleurs compétiteurs pour prélever les nutriments que les plantes. Conséquemment, celles-ci absorbent la majorité de leurs nutriments après que les micro-organismes aient absorbé assez de nutriments pour contrer leurs limites nutritionnelles. Par contre, dans une perspective à plus long terme, les plantes récupéreront la majorité des nutriments séquestrés

par les micro-organismes. Elles le feront via le bris des cellules microbiennes et le lessivage subséquent puisque les micro-organismes ont un cycle de vie beaucoup plus court que les plantes (Hodge *et al.* 2000). Nordin *et al.* (2004) ont montré que la biomasse microbienne récupère en moyenne 40 à 49 % de l'azote ajouté expérimentalement dans le sol d'une toundra arctique, tandis que moins de 1 % est récupéré par les plantes et ce, quatre heures après l'ajout. Le reste de l'azote est lessivé. De leur côté, Marion *et al.* (1982) ont montré que 79 % du ^{15}N ajouté est récupéré par la biomasse microbienne comparativement à 16 % pour les plantes vasculaires après deux mois. Ce qui semble confirmer l'avantage des micro-organismes dans la compétition pour les nutriments. La quantité de nutriments disponible pour les plantes est donc généralement directement liée à celle relâchée par les micro-organismes durant les baisses périodiques de leur population (Chapin *et al.* 1978; Jonasson *et al.* 1996). Les plantes pourraient compenser pour leur faible capacité de compétiteurs contre les micro-organismes en absorbant directement des acides aminés du sol. En effet, la glycine est un substrat peu efficace pour la croissance des micro-organismes tout en étant relativement abondante dans les milieux arctiques et les plantes sont capables de l'absorber rapidement (Lipson *et al.* 1999). Les quantités élevées de nutriments fixées dans la biomasse microbienne suggèrent donc que les cycles microbiens de minéralisation et d'immobilisation sont extrêmement importants pour la dynamique saisonnière des nutriments dans les écosystèmes arctiques (Jonasson et Shaver 1999).

1.2 Relations entre les herbivores et les plantes

L'interaction entre les herbivores et les plantes est généralement l'interaction trophique dominante dans les écosystèmes arctiques (Gauthier *et al.* 1996). Sous les latitudes nordiques, les herbivores sont habituellement généralistes. Plusieurs herbivores sont cependant sélectifs dans leur quête alimentaire et ils sélectionnent ordinairement les plantes contenant beaucoup de nutriments solubles tout en étant faibles en fibres ou en composés secondaires (Manseau et Gauthier 1993). Le comportement d'alimentation dans ces écosystèmes est donc influencé par la disponibilité de la végétation avec une haute teneur nutritionnelle, mais aussi par les conditions abiotiques ou la diversité des espèces végétales (Jefferies *et al.* 1994). Les herbivores se déplaceront aussi beaucoup pour exploiter les

endroits où il y a des hausses temporelles et spatiales de productivité car les environnements arctiques ne peuvent pas maintenir des taux élevés de recyclage des éléments nutritifs (Jefferies *et al.* 1994).

À première vue, le broutement devrait avoir un impact négatif pour la croissance des plantes en diminuant, par exemple, leur biomasse aérienne. Pourtant, dans certains cas, un broutement modéré peut favoriser une reprise rapide de la croissance. Ainsi, les plantes broutées d'un marais subarctique ont une plus grande production primaire que celles non broutées (Cargill et Jefferies, 1984b; Hik et Jefferies 1990). En fait, pour que le broutement favorise la croissance des plantes dans un écosystème donné, deux conditions sont nécessaires : la quantité de nutriments qui entrent dans le système doit être suffisante pour répondre aux besoins des plantes et les herbivores doivent contribuer à améliorer la conservation des nutriments dans le système (De Mazancourt et Loreau 2000). Un broutement modéré peut aussi permettre de maintenir la quantité et la qualité des plantes broutées (Ngai et Jefferies 2004) alors que dans certains cas, le broutement modéré n'a que peu d'impact sur la productivité des plantes (Zellmer *et al.* 1993; Gauthier *et al.* 1995). Cependant, lorsque le broutement devient trop intense, le milieu peut être fortement perturbé et dégradé (Kerbes *et al.* 1990; Kotanen et Jefferies 1997; Jano *et al.* 1998). Et parfois, même une faible intensité de broutement peut altérer les communautés végétales et affecter la disponibilité du fourrage (Zacheis *et al.* 2001). Bien des herbivores se nourrissent de rhizomes ou de racines plutôt que des parties aériennes et ce type de broutement a généralement un impact négatif sur la dynamique de l'écosystème (Iacobelli et Jefferies 1991; Bélanger et Bédard 1994). La fréquence du broutement aura aussi un impact non négligeable sur la capacité des plantes à contrer ses effets (Beaulieu 1995).

Selon McNaughton (1983), il existe trois types de réponses par les plantes après qu'elles aient subi un stress dû au broutement : 1) une baisse de la croissance (sous-compensation), 2) le remplacement des tissus broutés (compensation) et 3) une hausse de la croissance des plantes broutées comparativement à celles non broutées (sur-compensation). Ainsi, les plantes réagissent différemment au broutement. Certaines sont sensibles au broutement et ne sont pas capables de récupérer alors que d'autres le tolèrent grâce à des mécanismes favorisant la reprise rapide de la croissance ou l'évitent en synthétisent des produits

secondaires toxiques ou difficilement digérables comme réaction de défense (Rosenthal et Kotanen 1994). Finalement, pour réduire l'effet du broutement, il semblerait que la meilleure stratégie serait d'avoir un cycle vital court (van der Meijden *et al.* 1988).

Il peut être avantageux pour les plantes d'être broutées pour plusieurs raisons : 1) l'élimination des tissus âgés, 2) la réduction de la sénescence, 3) la translocation de nutriments des parties non broutées vers celles broutées, 4) l'augmentation de l'activité photosynthétique des parties restantes, 5) l'accès à des nutriments facilement assimilables via les déchets organiques des herbivores, 6) la redistribution hormonale ou 7) la stimulation de la croissance par des substances présentes dans la salive des herbivores (McNaughton 1979). Les herbivores peuvent donc améliorer eux-mêmes la qualité de leur nourriture (Ruess *et al.* 1997; van der Wal *et al.* 2004). Le modèle de De Mazancourt et al. (1998) montre que les herbivores peuvent maximiser la production primaire d'un écosystème à des intensités de broutement modérées. Il semble même que les herbivores puissent modifier les processus écosystémiques et atténuer les déficiences en nutriments à un point tel qu'ils pourraient augmenter la capacité de support de leur milieu (McNaughton *et al.* 1997). Le broutement peut aussi favoriser les successions végétales. Par exemple, en Norvège, le broutement intensif par les rennes (*Rangifer tarandus platyrhynchus* Vrolik.) aide à la transition d'une toundra dominée par les mousses vers une steppe beaucoup plus productive dominée par les plantes graminoides (Olofsson *et al.* 2001). D'abord, le broutement et le piétinement par les herbivores y réduisent la profondeur de la couche de mousses, ce qui augmente la température du sol et favorise la croissance des plantes vasculaires (van der Wal *et al.* 2001). Ensuite, les plantes graminoides sont directement favorisées par l'ajout additionnel de nutriments provenant des fèces et de l'urine (van der Wal et Brooker 2004; van der Wal *et al.* 2004). En revanche, le broutement peut être essentiel au maintien d'un écosystème, comme par exemple pour la savane africaine.

En plus des processus mentionnés plus haut favorisant la reprise de la croissance suite au broutement, il a été observé que les fèces ou l'urine relâchées par les herbivores sur les milieux broutés peuvent accroître la croissance des plantes vasculaires (McNaughton 1979; Semmartin et Oesterheld 2001; van der Wal et Brooker 2004). Dans certains cas, les fèces sont même indispensables pour que les plantes puissent récupérer suite au broutement

(Mckendrick *et al.* 1980; Bazely et Jefferies 1985; Ruess *et al.* 1989; Hik *et al.* 1991). En fait, les herbivores court-circuitent le cycle des nutriments en rendant rapidement disponible une certaine quantité d'azote inorganique (Ruess *et al.* 1997) ou organique (acides aminés) (Henry et Jefferies 2003a) hautement solubles et facilement assimilables par les plantes. Plus précisément, le relâchement d'éléments nutritifs par les fèces court-circuite le processus de décomposition microbienne, celui-ci étant particulièrement lent en Arctique à cause des faibles températures. Par contre, dans certains cas, les fèces n'ont pas d'effet sur la disponibilité des nutriments. Ceci pourrait être causé par les faibles densités d'herbivores présentes dans le milieu (Zacheis *et al.* 2002a) ou par la présence d'un tapis de mousse tel que suggéré par Gauthier *et al.* (1996). D'autres activités des herbivores peuvent aussi accélérer le recyclage des nutriments. Par exemple, dans un marais salant en Alaska, le piétinement par les oies incorpore de la litière dans le sol, ce qui résulte en une augmentation des taux de décomposition et de minéralisation. Il crée aussi des trouées dans la végétation, ce qui forme des habitats propices à la prolifération des cyanobactéries fixatrices d'azote (Zacheis *et al.* 2002b). Au contraire, Ritchie *et al.* (1998) ont démontré que le recyclage de l'azote était indirectement ralenti par les herbivores car ceux-ci diminuent l'abondance des espèces de plante avec des tissus riches en N. En fait, le comportement des populations d'herbivores influencera la réponse du cycle des nutriments. Une espèce ayant des pics de population importants suivis d'une période avec un nombre d'individus beaucoup plus faible, comme les lemmings ou les campagnols, risque beaucoup plus de ralentir le cycle des nutriments car les individus consommeront une quantité importante de végétaux sur une courte période de temps. Sirotnak et Huntly (2000) ont démontré que la minéralisation de l'azote est ralentie pour une longue période car la qualité de la litière des espèces avec beaucoup d'azote dans leurs tissus, comme les légumineuses, est diminuée par le broutement intensif des campagnols durant les pics de population dans le Parc National de Yellowstone, au Wyoming. Une espèce d'herbivore ayant une population relativement constante dans le temps évitera plutôt d'affaiblir la qualité de son milieu en se déplaçant fréquemment par exemple. De plus, avec le temps, l'effet positif des fèces ou des activités des herbivores sur le recyclage des éléments nutritifs peut devenir inexistant si la pression de broutement devient trop élevée. C'est présentement le cas dans le Parc National des Montagnes Rocheuses, au Colorado, où les densités d'ongulés sont

trop élevées (Singer et Schoenecker 2003) ou à La Pérouse Bay, au Manitoba, où la population d'oies a complètement dévasté son habitat (Kotanen et Jefferies 1997; Jano *et al.* 1998). Dans d'autres cas cependant, il doit y avoir un broutement intensif pour que le cycle des nutriments soit favorisé (Olofsson *et al.* 2001). En effet, Olofsson *et al.* (2004) ont démontré que sous des intensités de broutement élevées par les rennes dans les steppes de Norvège, la production primaire est favorisée par l'augmentation du recyclage des nutriments et ce, même dans une perspective à long terme sur une échelle de temps écologique.

1.3 Un cas spécifique : la Grande oie des neiges et l'île Bylot

La population de la Grande oie des neiges (*Chen caerulescens atlantica* L.) a considérablement augmenté depuis les 40 dernières années. Cette augmentation semble être reliée à la diminution de la mortalité sur les sites d'hivernage de la côte est des États-Unis et à l'utilisation croissante des terres agricoles qui fournissent des grains ayant un plus haut rendement énergétique que leur nourriture habituelle (Gauthier *et al.* 2005). Cette espèce fait deux haltes migratoires dans l'estuaire du fleuve Saint-Laurent à chaque année, une au printemps pour aller se reproduire plus au Nord et l'autre à l'automne pour aller vers leur site d'hivernage. La population mondiale est passée d'environ 30 000 individus en 1965 à environ 960 000 individus en 2004 (Fig. 1.1; Reed *et al.* 1998 et Service Canadien de la Faune, données non publiées).

L'île Bylot, située dans le Haut-Arctique canadien (73°08' N - 80°00' W), est le site principal de nidification de la Grande oie des neiges (Reed *et al.* 1992; Gauthier *et al.* 1996). Environ 15 % de la population mondiale niche sur l'île à chaque été (Reed *et al.* 1992). En 2004, environ 144 000 individus se sont reproduits sur la plaine sud de l'île. Le reste de la population se reproduit sur plusieurs sites répartis dans l'Est du Haut Arctique canadien, du Nord de la terre de Baffin au Nord de l'île d'Ellesmere. Quelques oiseaux nichent également dans l'Ouest du Groenland (Études écologiques et suivi environnemental à l'île Bylot, Parc National Sirmilik, 15 mars 2006) Le taux de succès de la nidification pour l'été 2004 s'établissait à 0,94 jeune par adulte. Il y avait donc environ 279 000 oies qui broutaient sur l'île cet été-là. Massé *et al.* (2001) ont établi que la capacité de support

des milieux humides, l'habitat préférentiel des oies pour leur alimentation (Gauthier 1993), est de 341 000 oies.

Les milieux humides ne représentent qu'environ 11 % de la superficie de la plaine sud de l'île Bylot (plaine sud = 1 600 km²) où nichent les oies (Hughes *et al.* 1994). Cette aire est caractérisée par une mosaïque d'habitats humides d'eau douce composée de polygones de tourbe, de petits lacs, d'agrégations d'étangs et de mares (Massé *et al.* 2001; Ellis et Rochefort 2004). Tous ses habitats sont entourés par une toundra mésique et, avec l'altitude, de collines et montagnes rocheuses dépourvues de végétation. Les polygones de tourbe (Fig. 1.2) et les ruisseaux sont les milieux humides de l'île les plus utilisés par l'oie (Massé *et al.* 2001). Un polygone de tourbe est désigné par une surface modelée par l'action du gel et du dégel des coins de glace et caractérisée par un bourrelet surélevé et sec entourant un centre humide mal drainé. Selon Ellis et Rochefort (2004), la formation des polygones de tourbe est fortement reliée aux processus géomorphologiques. Lorsque les coins de glace sont actifs sous l'influence d'un climat froid, les bourrelets des polygones deviennent plus élevés. Le centre des polygones s'humidifie également car l'eau peut s'y accumuler. L'emprisonnement des sédiments transportés par le vent y est aussi plus important. Ceci favorise la croissance des mousses ainsi que l'accumulation de la tourbe. Si la tourbe s'accumule plus rapidement que le soulèvement des bourrelets extérieurs, le centre du polygone devient plus sec car l'eau est retenue plus difficilement. L'accumulation de la matière organique diminue alors et les bourrelets s'élèvent à nouveau plus rapidement, ce qui recommence le cycle. Le centre des polygones peut donc être convexe (généralement sec) ou concave (généralement humide). Le centre des polygones concaves est constitué, selon sa profondeur, d'une mare ou d'une tourbière minérotrophe (*fen*). Les plantes vivant à l'intérieur des polygones concaves reçoivent leurs nutriments des précipitations et du ruissellement à la fonte des neiges. Les fens et la bordure des mares sont recouverts de plantes graminoides comme *Carex aquatilis* var *stans* Drej., *Dupontia fisheri* R. Br. et *Eriophorum scheuchzeri* Hoppe qui poussent au-travers d'un tapis de mousse dense et continu dominé par *Drepanocladus revolvens* (Sw.) Warnst. Le saule arctique (*Salix arctica* Pall.) domine sur les parties plus sèches des polygones de tourbe.

À leur arrivée printanière sur l'île Bylot, les oies s'alimentent dans les habitats exposés, là où la neige fond plus rapidement (Gauthier 1993). Lorsque les milieux humides commencent à être accessibles suite à la fonte des neiges, les oies vont principalement consommer les parties souterraines des plantes (*grubbing*) (Gauthier 1993). Cependant, durant l'été, les oies se nourrissent presque exclusivement des parties aériennes des plantes vasculaires graminoides présentes dans les milieux humides (Massé 1998). La pression de broutement augmente considérablement sur ces milieux en juillet suite à l'éclosion des oisons (Gauthier *et al.* 1995; Beaulieu *et al.* 1996). Finalement, à la fin de l'été, lorsque la qualité nutritive des plantes des milieux humides décline, les oies retournent s'alimenter dans les milieux mésiques des collines (Duclos 2002). Les plantes les plus consommées dans les milieux humides sont *Eriophorum scheuchzeri* et *Dupontia fisheri*. Entre 65 et 100 % de la production primaire d'*Eriophorum scheuchzeri* est consommée chaque année. Pour *Dupontia fisheri*, les chiffres se situent plutôt entre 30 et 78 % (Gauthier *et al.* 1995). En fait, toutes espèces confondues, le broutement par les oies prélève environ 40 % de la production primaire annuelle de ces milieux bon an, mal an. Les oies contribuent à maintenir un équilibre dans lequel la production de plantes graminoides est plus faible comparativement à la situation où les oies seraient absentes du système (Gauthier *et al.* 2004). Les espèces de linaigrettes (genre *Eriophorum*) sont davantage broutées car elles contiennent significativement 20 % plus d'azote et 25 % moins de fibres que les autres espèces broutées (Gauthier 1993; Manseau et Gauthier 1993). L'analyse de contenus stomacaux d'oies a montré que les mousses, quant à elles, ne sont pas broutées directement par les oies. Une petite quantité est ingérée par accident lorsque les plantes vasculaires sont broutées (Gauthier 1993).

Le broutement à long terme a un impact significatif sur les plantes graminoides des milieux humides de l'île Bylot. Les espèces broutées préférentiellement voient leur biomasse aérienne diminuer comparativement aux mêmes espèces non soumises au broutement (Gauthier *et al.* 1995). Au contraire, un broutement modéré n'a presque pas d'impact sur la production primaire des plantes vasculaires des milieux humides et celles-ci ne répondent pas aux nutriments relâchés par les fèces (Beaulieu *et al.* 1996). Il semble que l'azote libéré par les fèces d'oies ne soit pas immédiatement disponible pour les plantes vasculaires à cause du tapis de bryophytes couvrant les polygones de tourbe. Gauthier *et al.* (1996) ont

suggéré que les bryophytes agiraient comme une barrière biologique au passage des nutriments, peut-être parce qu'ils ont une capacité d'échange ionique très élevée (Clymo 1963; Craigie et Maass 1966). Suite à des analyses réalisées avec un isotope d'azote radioactif (^{15}N) dans les milieux humides de l'île Bylot, Kotanen (2002) a démontré que les mousses semblent absorber le ^{15}N au détriment des racines des plantes vasculaires. Les bryophytes semblent séquestrer l'azote provenant des fèces, qui autrement aurait été facilement assimilable par les plantes. Dans une perspective à long terme, cela pourrait réduire la capacité de récupération des plantes broutées suite aux dommages faits par l'oie. Finalement, un changement de l'abondance relative et de la biomasse des espèces est observé lorsque des parcelles de végétation sont protégées du broutement (Gauthier *et al.* 1996). En effet, après 5 ans, *Eriophorum scheuchzeri* devient l'espèce dominante des parcelles protégées et voit sa biomasse tripler. La Grande oie des neiges contribue donc à modifier l'écosystème des milieux humides de l'île Bylot et il n'y a pas d'évidence d'un feed-back positif du broutement comme c'est le cas dans d'autres écosystèmes. Les plantes vasculaires répondraient au broutement par une croissance sous-compensatoire (Gauthier *et al.* 1995). En fait, les plantes broutées sont capables de développer des nouvelles feuilles suite au broutement, mais sans ne jamais atteindre les niveaux de biomasse obtenus par les mêmes espèces lorsqu'elles ne sont pas broutées. Il est ainsi important d'étudier l'effet fertilisant de l'herbivorisme par l'oie sur les plantes graminoides et les bryophytes par l'ajout de nutriments pour comprendre la dynamique complexe entre les oies, les plantes broutées et les mousses dans les milieux humides de l'île.

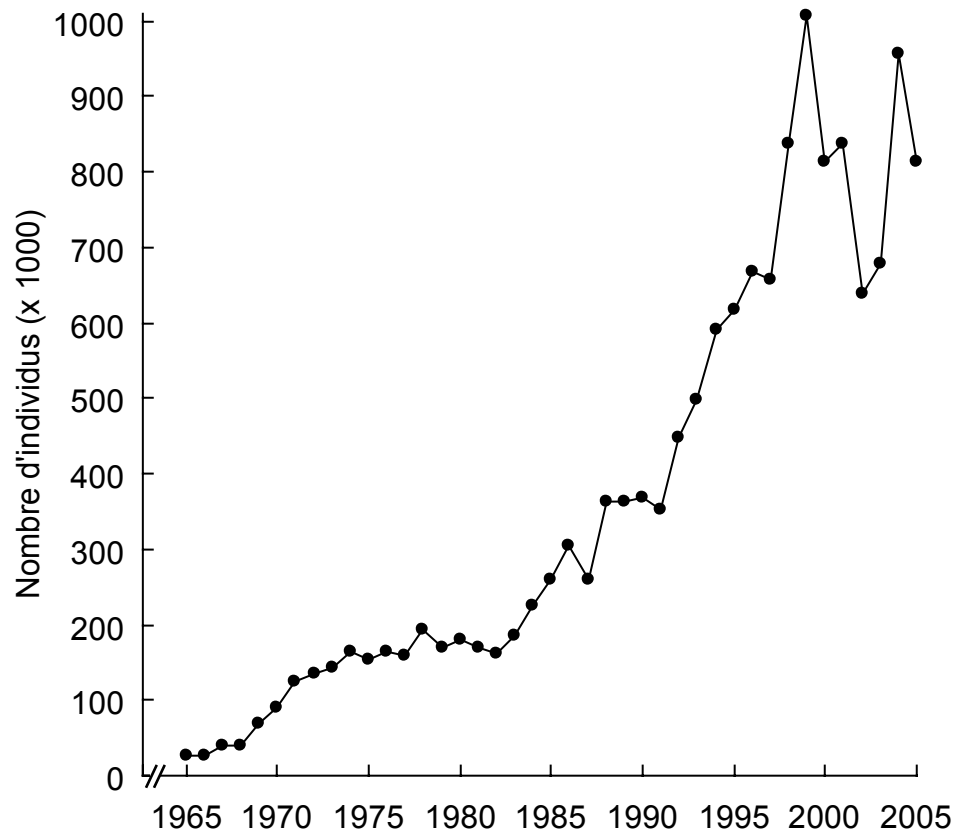


Figure 1.1 Nombre d'individus constituant la population de la Grande oie des neiges au printemps sur les rives de l'estuaire du Saint-Laurent (entre 1965 et 1998, Reed *et al.* 1998 ; entre 1999 et 2005, Service canadien de la faune, données non publiées).



Figure 1.2 Photographie représentant deux types de polygones de tourbe sur l'île Bylot. Les flèches noires pleines indiquent des polygones avec le centre humide et concave tandis que la flèche pointillée montre un polygone avec le centre sec et concave.

1.4 Études de fertilisation dans les milieux arctiques

Que ce soit à l'île Bylot ou ailleurs en Arctique, plusieurs études de fertilisation ont été menées pour simuler l'ajout de nutriments par les herbivores ou pour déterminer l'élément nutritif le plus limitant dans un écosystème arctique donné (Haag 1974; Mckendrick *et al.* 1978; Bazely et Jefferies 1985; Henry *et al.* 1986; Hik *et al.* 1991; Kielland et Chapin 1994; Shaver et Chapin 1995; Pineau 1999; Kotanen 2002, Henry et Jefferies 2003b). L'augmentation d'un des paramètres servant à estimer la croissance après l'addition d'un nutriment est utilisée pour indiquer une déficience de ce nutriment particulier dans le milieu étudié. L'effet fertilisant de l'herbivorisme est testé sur la productivité primaire des plantes vasculaires ou des bryophytes, ainsi que sur le contenu en azote et en phosphore présent dans les plantes. Même si les réponses des plantes vasculaires à une fertilisation azotée (Haag 1974; Mckendrick *et al.* 1978; Shaver et Chapin 1995), phosphorée (Mckendrick *et al.* 1978; Kielland et Chapin 1994; Shaver et Chapin 1995), à une combinaison d'azote et de phosphore (Haag 1974; Mckendrick *et al.* 1978; Henry *et al.* 1986; Hik *et al.* 1991; Shaver et Chapin 1995), aux fèces (Bazely et Jefferies 1985; Hik *et al.* 1991) ou aux acides aminés (Henry et Jefferies 2003b) sont généralement positives, celles-ci sont très variables selon les études. Dans certains cas, il semble que les bryophytes profitent davantage de l'enrichissement comparativement aux plantes vasculaires. En effet, les bryophytes répondent à des doses plus faibles que celles nécessaires pour obtenir une réponse des plantes vasculaires (Pineau 1999; Kotanen 2002). Par contre, dans certains cas, la fertilisation peut avoir un effet contraire. Par exemple, il semble que la croissance de plusieurs espèces de bryophytes dans les pays scandinaves soit affectée par des doses trop élevées de nutriments ($> 5 \text{ g de N / m}^2$ par année) (Tomassen *et al.* 2003). Ainsi, il arrive fréquemment que la biomasse ou le couvert des bryophytes diminuent suite à la fertilisation tandis que ceux des plantes vasculaires (principalement les plantes graminoides) augmentent (e.g. Graglia *et al.* 2001; Granberg *et al.* 2001; Grellmann 2002; Pauli *et al.* 2002; Bret-Harte *et al.* 2004). L'ajout de nutriments permet donc aux plantes vasculaires d'avoir une meilleure croissance en augmentant la disponibilité des éléments nutritifs dans la rhizosphère puisque les bryophytes atteignent leur niveau de saturation en nutriments à des doses relativement faibles (Limpens *et al.* 2003). En retour, l'augmentation de l'abondance des plantes vasculaires dans les milieux humides après l'ajout de nutriments

peut avoir des conséquences dramatiques sur ces écosystèmes. L'ombrage causé par l'augmentation de la croissance des plantes vasculaires et de la litière a un impact direct sur la productivité des bryophytes puisque l'intensité lumineuse atteignant la strate muscinale s'en trouve diminuée. En fait, l'ajout d'une quantité donnée d'azote favorise les sphaignes lorsque les plantes vasculaires sont coupées, mais leur nuit lorsque les densités de plantes vasculaires sont trop importantes (augmentation de l'ombrage) (Hogg *et al.* 1995; Malmer *et al.* 2003). Une même conclusion ressort généralement de ces études, soit que la deuxième année après la fertilisation est reconnue pour bien intégrer les effets à court terme d'applications de nutriments dans la toundra arctique (Pineau 1999).

Bien qu'intéressantes, ces études soulèvent cependant certaines questions. En effet, pour toutes ces études, l'application de fertilisants ne s'est faite qu'une seule fois. La réponse des plantes était évaluée l'année de l'ajout de nutriments ou après plusieurs saisons de croissance (entre 2 et 10 saisons). L'apport provenant des herbivores n'est pas bien représenté dans ce type d'étude car les herbivores fournissent un apport continu et annuel de nutriments dans le milieu. Par ailleurs, pour plusieurs de ces études, les unités expérimentales étaient souvent très proches les unes des autres. Des problèmes peuvent ainsi subvenir s'il y a, par exemple, de fortes pluies et du ruissellement. La réponse des plantes d'une unité expérimentale peut alors être influencée par les traitements appliqués dans celles adjacentes.

1.5 Contexte de l'étude

Les écosystèmes des régions arctiques font partie des écosystèmes terrestres les plus fragiles. Les conditions abiotiques présentes dans ces milieux font en sorte que ceux-ci peuvent difficilement s'adapter aux perturbations, qu'elles soient d'ordres climatiques ou biologiques. De plus, comme le lien trophique entre les plantes et les herbivores est à la base des interactions présentes dans plusieurs écosystèmes, une augmentation des populations d'herbivores dans les écosystèmes arctiques peut causer des changements dramatiques. Cela peut même aller jusqu'à la destruction du milieu, comme ce fut le cas le long de la Baie d'Hudson (Kerbes *et al.*, 1990). L'île Bylot n'y échappe pas. Même si la population de la Grande oie des neiges nichant sur l'île a légèrement diminué suite à

l'instauration de la chasse de printemps en 1999 (la population s'élevait à 52 000 individus en 1983, Reed et Chagnon 1987; 73 100 individus en 1988, Reed *et al.* 1992; 156 000 individus en 1993 et 106 000 individus en 2003, Service Canadien de la Faune, données non publiées), les milieux humides de l'île sont encore très utilisés par les oies pour leur quête alimentaire. Les oies contribuent à l'enrichissement de cet écosystème par leurs fèces en plus d'y accélérer le recyclage des éléments nutritifs. Il est à noter que les oies n'augmentent pas la quantité de nutriments présents dans le milieu, mais elles changent plutôt la forme de ceux-ci. Les oies transforment les nutriments provenant des plantes en composés hautement solubles et facilement assimilables, court-circuitant ainsi une partie du recyclage des nutriments qui se fait habituellement via la décomposition lente des plantes. Une étude de fertilisation à long terme dans les polygones de tourbe permettrait donc d'en apprendre davantage sur la réponse des plantes les plus broutées et sur le rôle précis des oies dans le recyclage des éléments nutritifs et dans les processus de décomposition. Le rôle des bryophytes dans les milieux humides de la toundra arctique est souvent négligé, alors qu'il doit être étudié pour mieux évaluer son impact dans la récupération des plantes graminoides suite au broutement (Kotanen, 2002). Une attention particulière sera ainsi donnée au rôle de la strate muscinale dans les interactions trophiques présentes dans les polygones de tourbe.

L'originalité de la présente étude, comparativement aux autres études de fertilisation déjà faites en Arctique, est que l'ajout de nutriments de la plupart des traitements est fait de manière répétitive à tous les ans depuis 2003 et le sera jusqu'en 2007 (soit sur une période de 5 ans), ce qui reflète davantage l'impact annuel d'un herbivore. De plus, les unités expérimentales sont distantes d'au moins 5 mètres et les blocs de plusieurs centaines de mètres, ce qui permet de réduire considérablement les biais possibles liés au ruissellement.

La production primaire des plantes des milieux humides arctiques est stimulée par des taux de fertilisation annuels qui varient entre 1 et 10 g / m² pour le N et 0,3 et 2,5 g / m² pour le P (Pineau, 1999), les traitements de fertilisation ont ainsi été ciblés pour couvrir ces intervalles tout en demeurant proches de la réalité, soit la quantité de nutriments trouvée dans les fèces d'oie (environ 2,5 % de N et 0,5 % de P, Beaulieu 1995). Puisque certains

traitements sont appliqués à chaque année et d'autres, seulement la première année de l'étude, il était possible de comparer l'impact d'une dose unique de fertilisants selon l'approche traditionnelle par rapport à des doses annuelles sur le recyclage des éléments nutritifs et la productivité de cet écosystème, tout en tenant compte de la présence des mousses. Cette étude nous permet de comprendre les effets à court terme de l'ajout de nutriments dans les milieux humides de l'île. Comme l'ajout de nutriments se fera pendant 5 ans, un autre projet en étudiera les effets à long terme. Ces études permettront d'augmenter les connaissances sur les interactions trophiques dominantes dans les milieux humides de l'île Bylot, ce qui aidera à préserver adéquatement cet écosystème arctique fragile.

1.6 Objectifs et Hypothèses de recherche

L'objectif général du premier chapitre était de comprendre l'influence de la Grande oie des neiges sur la production primaire des plantes graminoides et des mousses, les taux de décomposition et le recyclage des éléments nutritifs dans les polygones de tourbe de l'île Bylot par l'application de différents traitements de fertilisation. Les buts étaient 1) de confirmer la nature des limites nutritionnelles présentes dans ce milieu, 2) d'estimer l'effet fertilisant des fèces d'oie et 3) de clarifier les interactions trophiques dans cet écosystème entre les oies, les plantes graminoides broutées et les mousses. Les hypothèses de recherche étaient les suivantes :

- 1) Selon Pineau (1999), la croissance des plantes graminoides est limitée par le N, mais pas par le P. Par contre, celle des mousses n'est pas limitée ni par le N, ni par le P. Même en utilisant des traitements de fertilisation moins démarqués (1 et 10 de N g / m² pour l'étude de Pineau vs 1, 3 et 5 de N g / m² pour cette étude), les mêmes limites nutritionnelles s'exprimeront.
- 2) La croissance des plantes graminoides et des mousses sera davantage favorisée par les additions combinées de N et de P comparativement à l'un ou l'autre des nutriments ajouté seul.

- 3) L'ajout de glycine favorisera davantage la croissance des plantes graminoides et des mousses qu'un ajout équivalent de N inorganique (1 g / m²) puisque les acides aminés peuvent être incorporés directement dans les processus de croissance (Kielland 1997; Henry et Jefferies 2003b).
- 4) L'ajout de fèces aura le même effet qu'un ajout équivalent de N (1 g / m²) sur la croissance des plantes graminoides ou des mousses.
- 5) Selon l'hypothèse du tapis de bryophytes émises dans Gauthier *et al.* (1996), les mousses bénéficieront de l'apport soudain de nutriments provenant des dépositions de fèces d'oie en augmentant leur croissance annuelle et en séquestrant les nutriments au détriment des plantes graminoides. Ainsi un apport en nutriments semblable à celui provenant des fèces d'oie favorisera la production des bryophytes, mais pas celle des plantes graminoides.
- 6) Les bryophytes deviendront saturées en nutriments suite à l'addition des doses les plus élevées en fertilisants. Selon cette hypothèse, il devrait avoir une augmentation du contenu en N ou en P dans les tissus des bryophytes et une amélioration de la croissance des plantes graminoides au fur et à mesure que les additions de nutriments augmenteront.
- 7) Les taux de décomposition et les recyclages des éléments nutritifs seront favorisés par l'augmentation des doses de nutriments. En fait, les micro-organismes auront accès à une plus grande réserve de nutriments, accélérant ainsi la décomposition de la matière organique.

L'objectif général du second chapitre était d'identifier les limites des méthodes servant à estimer l'élongation des tiges de bryophytes dans les conditions difficiles de croissance présentes dans le Haut-Arctique. Les buts étaient 1) de tester une nouvelle variante d'une méthode déjà utilisée pour la croissance des bryophytes, mais jamais testé en milieux arctiques, i.e. faire des marques avec un marqueur permanent à un même niveau sur chaque tige, 2) de comparer cette méthode avec d'autres déjà utilisées dans le passé dans cet

environnement (tiges coudées et marqueurs naturels) et 3) de suggérer la meilleure méthode à utiliser selon les contraintes de l'écosystème ou des conditions de travail.

Chapitre 2

Nutrient dynamics in arctic wetlands: moss layer constrains the fertilizing effects of Greater snow geese in polygon fens on Bylot Island, Nunavut.

Rémy Pouliot, Line Rochefort, Chantal Pineau & Gilles Gauthier

2.1 Résumé

Les herbivores peuvent affecter positivement les habitats dans lesquels ils se nourrissent par leurs fèces en y accélérant le recyclage des nutriments. Par contre, les tapis de mousse constituent souvent une composante majeure des écosystèmes de toundra et ils peuvent modifier l'effet des herbivores. Par l'ajout de nutriments, nous avons étudié les nutriments limitant la croissance des mousses et des plantes graminoides ainsi que l'effet fertilisant de la Grande oie des neiges sur la production primaire des plantes graminoides et des mousses, les taux de décomposition et le recyclage des nutriments au niveau des racines. L'azote limite la croissance des plantes graminoides, mais pas celle des mousses et le phosphore n'est pas limitant pour ces deux groupes de plantes. Avec des doses d'azote semblables à l'apport des fèces d'oie ($1 \text{ g} / \text{m}^2$), les mousses agissent comme une barrière naturelle en absorbant les nutriments. Avec des doses d'azote plus élevées ($5 \text{ g} / \text{m}^2$), les mousses sont saturées et le surplus des nutriments est lessivé jusqu'aux racines des plantes graminoides. Dans les polygones de tourbe avec un tapis de mousse dense, les mousses modifient ainsi l'interaction herbivore- plante en séquestrant les nutriments ajoutés par les fèces et ont un effet négatif indirect sur les plantes broutées. Les taux de décomposition ne sont pas affectés par l'ajout de nutriments. Éventuellement, les nutriments devraient devenir disponibles via la décomposition des mousses et être graduellement transférés aux racines.

2.2 Abstract

Herbivores can positively affect their feeding habitat by releasing faeces and accelerating the nutrient turnover. However, moss carpets are often major components of tundra ecosystems and they can influence herbivore effects. By nutrient additions, we studied the nutrients limiting the growth of mosses and graminoid plants and the fertilizing effects of Greater snow geese on primary production of graminoid plants and mosses, decomposition rates and nutrient turnover at root levels. Graminoid plants showed nitrogen limitation, but mosses seemed to have no nitrogen or phosphorus limitation. Under N additions similar to natural loads from goose faeces (1 g / m²), mosses acted like a natural barrier by uptaking nutrients. At high level of N addition (5 g / m²), mosses were saturated and nutrient surplus could be leached down to roots and became accessible for graminoid plants. In polygon fens with a dense carpet of mosses, the trophic interaction between herbivores and plants was modified because mosses sequester the nutrients added by faeces and have an indirect negative effect on grazed plants. Decomposition rates were not affected by nutrients additions. With time, nutrients should slowly become available from the moss layer through decomposition and gradually transferred to the roots.

2.3 Introduction

Greater snow goose (*Chen caerulescens atlanticus* L.) population has considerably increased in the last decades (approximately 25 000 geese in 1965 and 960 000 in 2005 in the St. Lawrence River; Reed *et al.* 1998; Canadian Wildlife Service, unpublished data). As a consequence, their summer feeding habitats in the Arctic are subjected to a higher grazing pressure. On the other hand, geese could have a great fertilizing effect in these habitats since faeces density deposited on the soil also increases. Thus, it is important to better understand the trophic interactions between geese and wetlands, their preferred grazing habitat and, in this way, be able to act if changes occur in these fragile ecosystems.

It is well known that plant growth and distribution in the Arctic are strongly constrained by low radiation, low precipitation, low nutrient availability and the duration of snow-free period which is characterized by low air and soil temperatures. In turn, the low nutrient availability of arctic system is largely explained by low soil temperatures inhibiting the microbial activity which is essential to the decomposition and nutrient turnover processes (Henry & Jefferies 2003a). Thus, the productivity of tundra vegetation is strongly and consistently limited by mineral nutrient availability (Shaver & Chapin 1995). In fact, nitrogen (N) is often the primary limiting nutrient in most tundra plant communities, usually followed by phosphorus (P) (Hagg 1974; Chapin *et al.* 1975; Mckendrick *et al.* 1978; Shaver & Chapin 1980; Cargill & Jefferies 1984a; Henry *et al.* 1986). Nutrient availability influences also the nutritional quality of forage for herbivores (Ngai & Jefferies 2004).

Moreover, herbivores can influence the structure and species composition of their feeding habitat (Kerbes *et al.* 1990). More precisely, grazing can either lead to an enhancement or a reduction of plant production via a series of complex negative and positive feedbacks (McNaughton 1979). An enhancement of vegetation growth occurs when specific soil, plant and animal characteristics are met. These conditions include a lack of nutrients in the soil, an intense grazing effect with a rapid return of fecal nitrogen via herbivores and a quick turnover of nutrients in soil (Jefferies *et al.* 1994). Faeces and urine contain a high proportion of soluble nutrients that can be readily uptaken and assimilated by plants and

hence enrich the soil. According to Bazely and Jefferies (1985), 60% of the N from goose faeces is available to plants within 48 hours, and can thus be a major source of nutrient in nutrient-limited arctic ecosystems. The passage of plants through the digestive system of herbivores can counteract the limiting rate of nutrient release from litter decomposition (Ruess *et al.* 1989; Gauthier *et al.* 1996). This is especially true in the tundra ecosystems (Nadelhoffer *et al.* 1992). In some cases, this acceleration of nutrient cycling by herbivores improves the carrying capacity of their own habitat (McNaughton *et al.* 1997).

An example of a positive feedback following grazing was observed in the subarctic salt marsh at La Pérouse Bay, Manitoba. At this site, moderate grazing by Lesser snow geese (*Anser caerulescens caerulescens* L.) had a positive effect on primary production (Cargill & Jefferies 1984b). This was primarily due to the fertilizing effect of goose faeces (Bazely & Jefferies 1985; Hik & Jefferies 1990). The role of herbivore faeces in stimulating plant growth is not unique to the subarctic salt-marsh studied by Cargill and Jefferies (1984b). It is a well-known phenomenon in plant-herbivore systems (McNaughton, 1979). Faeces of reindeers (*Rangifer tarandus platyrhynchus* Vrolik) also positively influence the growth of vascular plants by promoting the soil nutrient cycling rate in an arctic steppe in Norway (Olofsson *et al.* 2004; van der Wal *et al.* 2004). The effect of grazing by Greater snow geese on primary production of graminoid plants has been determined in wetlands of Bylot Island in the Canadian High Arctic. Although grazed plants are able to produce new foliage, goose grazing does not enhance primary production (Gauthier *et al.* 1995; Beaulieu *et al.* 1996). In contrast with the saline marshes of La Pérouse Bay where most plants grazed by geese grow on mineral soil, plants found in polygon fens and pond margins of Bylot Island freshwater wetlands grow on organic soil formed mostly by bryophytes.

The bryophytes are often major components of tundra ecosystems (Clarke *et al.* 1971; Vitt & Pakarinen 1977). They are vital for ecosystem functions such as soil stabilization, erosion anticipation, soil moisture increase, soil and permafrost insulation, pollutant interception or enhancement of nitrogen fixation (Press *et al.* 1998). Even though an interaction between graminoid plants and mosses in nutrient cycling is a widely accepted idea, its relationship is not well understood (Shaver & Chapin 1995) and has often been

disregarded in studies of nutrient cycling in the Arctic (Longton 1984). In mosses, which do not have any root system, nutrient absorption occurs directly through the cellular surface. Further nutrition is also enhanced by leaf structure with one-cell thick and a high exchange capacity of the cell walls (Clymo 1963, 1973; Craigie & Maass 1966; Longton 1992). The absence of a positive response of graminoid plants to goose grazing in the wetlands of Bylot Island may be due to the moss carpet which could directly absorb or retain on their cell walls most nutrients leached from goose faeces (Kotanan 2002).

Two fertilisation trials conducted on Bylot Island in 1995-96 and 2003-04 are presented. A first objective was to examine the role of nutrients in limiting the growth of graminoid plants grazed by Greater snow geese and of mosses in polygon fens. An increase in one of the growth parameters measured following a nutrient addition was assumed to indicate a deficiency in that specific nutrient in polygon fens. The second objective was to estimate the fertilizing effects of goose droppings on primary production of graminoid plants and mosses, decomposition rates and nutrient turnover at graminoid plant root levels. The third objective was to clarify the trophic interactions between geese, graminoid plants and bryophytes in these polygon fens. We believe that mosses should benefit from a sudden pulse of nutrients coming from the deposition of goose faeces by increasing their annual growth and sequestering the nutrients at the detriment of graminoid plants (moss carpet hypothesis, Gauthier *et al.* 1996; Pineau 1999; Kotanan 2002).

2.4 Methods

The trial carried out in 1995-96 will be referred as the FTF experiment for first trial fertilization experiment and the 2003-04 experiment as the STF experiment for second trial fertilization experiment. The STF experiment will continue until 2007, here we show data after the first two growing seasons. Moss nomenclature follows Anderson *et al.* (1990).

2.4.1 Field site

The experiments were carried out in a glacial valley (50 km²) located on the southwest plain of Bylot Island, Nunavut, Canada (73°08' N - 80°00' W) (Fig. 2.1). This area is the main breeding site of the Greater snow goose population in the Arctic (Reed *et al.* 1992; Gauthier *et al.* 1996). In fact, approximately 15 % of the population uses Bylot Island as their breeding site each year (Reed *et al.* 1992). In 2004, almost 144 000 geese bred on the island (the total size of the population was near 960 000 individuals; Canadian Wildlife Service, unpublished data). In 1996 and 2004, there was respectively 0.83 and 0.94 gosling per adult (G. Gauthier, unpublished data). Then, about 181 000 geese grazed in 1996 in Bylot Island wetland. The estimation was about 279 000 geese in 2004. The site is characterized by a mosaic of freshwater wetland habitats composed of tundra polygon fens, small lakes and aggregations of ponds (Massé *et al.* 2001; Ellis & Rochefort 2004). These habitats are surrounded by upland tundra. Three different kinds of polygons, typically ranging from 10 to 20 m across, are present: high-centered polygon (mostly dry), low-centered polygon and flat meadow polygon. The basin of the low-centered and flat meadow polygons is characterized by a pond or a fen depending on its depth. Fens and pond margins are covered by graminoids such as *Carex aquatilis* var *stans* Drej., *Dupontia fisheri* R. Br. and *Eriophorum scheuchzeri* Hoppe and growing through a dense and continuous carpet of brown mosses dominated by *Drepanocladus revolvens* (Table 2.1). In dryer areas such as the middle portion of high-centered polygons, the surrounding ridges of low-centered polygon and the upland tundra, the arctic willow (*Salix arctica* Pall.) dominates with a very sparse graminoid cover (Gauthier *et al.* 1996). *D. fisheri* and *E. scheuchzeri* are the preferred food for geese in those wet habitats (Gauthier 1993; Manseau & Gauthier 1993;

Hughes *et al.* 1994; Gauthier *et al.* 1995). The active soil layer varies between 10 and 30 cm.

Springs of 1995 and 1996 were characterized by an important snow precipitation peak. On June 1st, average snow depths on polygon fens around camp were 52 cm in 1995 and 40 cm in 1996 (mean for the last decade, from 1995 to 2004, is 31 cm, G. Gauthier, unpublished data). Snowmelt was delayed and resulted in massive spring run off with extensive flooding of wetland areas in late June and beginning of July of both years. Averages for snow depth were 7 cm in 2003 and 22 cm in 2004. Field seasons of 1996, 2003 and 2004 were also wetter than normal. The rain precipitations were 130 mm in 1996, 122 mm in 2003 and 143 mm in 2004 (mean for the last decade, from 1995 to 2004, is 94 mm, G. Gauthier, unpublished data). In 1995, it fell 62 mm of rain.

2.4.2 Experimental design

In the first trial fertilization (FTF) experiment, a complete randomized block design of five blocks and eight treatments was used to test the effects of different N and P levels of fertilizer on plant production. Each block was situated in a fen polygon at least 500 meters separated from each other. Fertilizing treatments are summarized in Table 2.2. We established two controls: one with an enclosure and another one without. The amount of faeces deposited by geese through out one summer was estimated in 1993 at 10 faeces / m² with a goose population about 160 000 individuals (Gauthier *et al.* 1995). In 2004, the goose population was about 279 000 individuals and the amount of faeces deposited by geese through out this summer was evaluated at approximately 17.4 faeces / m². Then, the faeces density used in the experiment represented about 2.3 times the amount of faeces deposited by actual goose population. Since faeces treatment was not diluted in water, we used a higher faeces density than the natural one to be able to uniformly apply the treatment on experimental unit. Estimations of nutrients released from faeces are based on their chemical analyses. Total faecal N was 2.5 % and total P was 0.15 % per dried faeces and the average dried mass per faeces was 1 g (Beaulieu 1995). The low N treatment (1 g / m²) was equivalent to the amount of N in faeces treatment (40 faeces / m², Table 2.2) (40 faeces x 2.5 % = 1 g of N), which both corresponds to 2.3 times the annual loads of N income

from natural faeces densities. The high N and P treatment (10 g of N / m² and 3 g of P / m², Table 2.2) was based on the minimal dose that induced a positive response for graminoid plants in a similar habitat (Shaver and Chapin 1995). The low P treatment (0.6 g / m²) was used to have a NP treatment (10 g of N / m² + 0.6 g of P / m², Table 2.2) with equivalent addition by comparison with N and P percentage in faeces (16 times more N than P in faeces (Beaulieu 1995)). The NP treatment was 23 times higher than the annual loads of N and P income from actual faeces density. Fertilisation treatments were applied in 1995 and repeatedly in 1996 in exclosures (in plexiglas) of 60 cm in diameter and 30 cm high of which at least 20 cm was buried up to the permafrost to prevent leaching or external input of nutrients. All exclosures were installed at the end of August 1994 in order to reach maximum depth into the ground. Each block was protected from goose grazing with a chicken wire fence of 50 cm high with criss-crossing ropes on top.

In the second trial fertilization (STF) experiment, a complete randomized block design of six blocks and 14 treatments was used to test the effects of different type of nutrient addition. Each block was located in a fen polygon at least 500 meters separated from each other. Fertilizing treatments were applied once (in 2003 or in 2004) or twice (both years). Treatments are summarised in Table 2.2. We applied the same faeces treatment than for the FTF experiment. The glycine treatment was chosen because arctic plants are able to absorb amino acids directly from the ground (Kielland 1997; Henry & Jefferies 2003b) and polygon fens contain high concentrations of free amino acids (Atkin 1996; Henry & Jefferies 2002). Uptake rate of amino acids are negatively correlate with their molecular weight (Kielland 1994). Since glycine has the lowest molecular weight, it has the best absorption potential for plant (Chapin *et al.* 1993). The added dose of glycine was based on the dose added by Schimel and Chapin (1996) in a similar environment. They have showed that graminoid plant take out amino acid (glycine) more rapidly than NH₄⁺. Since we knew that the growth of graminoid plants was positively influenced by the addition of 10 g of N / m² and not influenced by the addition of 1 g of N / m² (Pineau 1999), we applied intermediate doses of N (3 and 5 g / m²) each year in this experiment (Table 2.2) to verify if graminoid plants respond positively at lower doses of N application (< than 10 g of N / m²). For P, we applied, each year, the same high dose (3 g of P / m²) than for the FTF experiment as well as an intermediate dose (1 g of P / m²) (Table 2.2). Doses applied only

one time were based on the long-term approach of the experiment (five years of fertilizer application). They corresponded to the nutrient addition total for five years of a particular dose that was and will be applied each year. Intermediate NP treatment (5 g of N / m² + 1 g of P / m²) was the combination of intermediate N and P treatments (Table 2.2). High NP treatment (15 g of N / m² + 2.5 g of P / m²) corresponded to the total of nutrient additions during five years of the low NP treatment (3 g of N / m² + 0.5 g of P / m²) but in a single dose. Each treatment was applied in 2 m x 2 m experimental units at least 5 meters separated from each others to prevent cross contamination between adjacent plots (Fig 2.2). All experimental units were installed at the end of June 2003, shortly after snowmelt. Each experimental unit was protected from goose grazing with a chicken wire fence of 50 cm high with crossing wires on top.

Nitrogen fertilizer (34-0-0) was applied as ammonium nitrate (NH₄NO₃) for both studies and phosphorus fertilizer as superphosphate (P₂O₅, 0-40-0) in the FTF experiment and as phosphoric acid (H₃PO₄, 0-46-0) in the SFT experiment. Applied quantity of glycin was calculated according to its nitrogen content. Glycin is constituted of 19 % of nitrogen. Goose faeces were collected fresh in the field less than one hour after being evacuated from defecating geese located with a scope. The faeces were collected with a spoon, stored in polyethylene bags and brought to the camp laboratory, weighed and systematically transferred in each experimental unit. For consistency, we approximated 500 g of fresh faeces as being 40 faeces. Nitrogen fertilizer, superphosphate and glycin were dissolved in water before application. All experimental units received 2 L of water / m². Faeces and phosphoric acid were uniformly put on moss surface before water application.

2.4.3 Graminoid plant and moss sampling

In the FTF experiment, six individual stems of graminoid plants (three of *D. fisheri* and three of *E. scheuchzeri*) were marked using modified paper clips of different colors to allow repeated measurements of leaf elongation (m) (green and total length; every seven days) and leaf counts per tiller at the end of the growing season (for the first year of fertilisation treatment only). We chose to present only cumulative green leaf elongation of individual tiller because it was easier to measure accurately as dead leaf tips sometimes fell due to

senescence and weathering (McKendrick *et al.* 1978). Since we were interested by the effect of nutrient additions on graminoid plants in general and not on a specific species, data for the two species were pooled before analyses and means per experimental unit were calculated.

For both experiments, aboveground phytomass was sampled during the peak of production (August 3rd in 1996 and between August 5th and 14th in 2004) by taking a 400 cm² piece of turf in 1996 and three 100 cm² of turf in 2004 in each experimental unit down to a depth of 10 cm for each sample (results were pooled by experimental unit). Aboveground phytomass sampled during the peak of production is a good approximation of net aboveground primary production (NAPP) in this ecosystem (Gauthier *et al.* 1995). Samples were stored in polyethylene bags in boxes protected from sun and rain under ambient temperature (~5°C). Sorting and drying were done within 4 days following sampling. We considered live aboveground phytomass only for grazed graminoids (i.e. *Carex aquatilis*, *D. fisheri* and *Eriophorum* spp.) because other vascular plants were not abundant (cover of ~0.5, Table 2.1). Aboveground parts included green leaves and green and white parts of the tiller above the last leafing node (see annexe 2 for details). Number of individual tillers (both experiments) and number of individual inflorescences (SFT experiment) were also counted for graminoid plants during the aboveground phytomass sorting to obtain tiller and inflorescence densities for each experimental unit. For the FTF experiment, we also measured leaf densities and we developed an index of growth with leaf elongation (E), number of leaves (N) and tiller density (TD):

$$\text{Index} = E * N * \text{TD} \quad (1)$$

To estimate primary production of graminoid plants, samples were dried at the field camp at 45°C for 24 h and stored in cardboard envelope. Due to logistic constraint, the material was brought back to the laboratory at Laval University (Quebec City), re-dried at 45°C until constant weight, kept in a desiccator and weighed to the nearest ± 0.001 g. All phytomass data were reported as dry mass.

Moss annual primary production (MAPP; in g / m²) was estimated with the following equation (Vitt & Pakarinen 1977):

$$\text{MAPP} = [W * G] / [SS * H] \quad (2)$$

where W is for moss dry biomass (g), G is for mean annual increment (m), SS is the sample surface (m²) and H is the mean moss living height (m). Under sharp distinct seasons such as in the High Arctic, several moss species show visible annual growth segment (Clarke *et al.* 1971; Vitt & Pakarinen 1977). On Bylot Island, *Polytrichum strictum* and *Meesia triquetra* have clear seasonal differences in leaf size and spacing between leaves. Those species were used as innate markers. As demonstrated in the next chapter, innate marker method is the best method to use to estimate moss primary production in arctic polygon fens when innate marker species are uniformly distributed. When it was possible, at least 15 stems of *P. strictum* or *M. triquetra* were collected in each experimental unit in mid-August of 1996 for the FTF experiment and between August 5th and 14th 2004 for the SFT experiment to measure annual increments (G) to the nearest ± 0.1 mm with an electronic vernier. For the FTF experiment, the surface sample (SS) was a 54 cm² piece of turf cored in the center of each enclosure (with an aluminium cylinder with sharp cutting edges). For the STF experiment, four turf samples of 22.5 cm² were cored and results were pooled by experimental unit before analyses. Living moss is composed of two parts, an upper green portion (photosynthetic active layer) and a lower brown portion (less active layer, down to the beginning of vascular plant roots). Estimates of biomass were done only with the green portion where the green moss layer height (H) was measured around each core at three different places in the FTF experiment and at 10 different places in the STF experiment. The green moss layer portion was cut, dried at 45°C for 24 h at the field camp and stored in cardboard envelope. Due to logistic constraint, the material was brought back to the laboratory at Laval University (Quebec City), re-dried at 45°C until constant weight, kept in a desiccator and weighed to ± 0.001 g. All phytomass data were reported as dry mass.

In the STF experiment, four quadrats (25 cm x 25 cm) were randomly surveyed in each experimental unit between August 5th and 14th 2004 to estimate the cover percentage of graminoid plants and bryophytes (data were pooled prior to statistical analyses).

2.4.4 Decomposition bag experimental design

To test the effect of nutrient addition on the decomposition of wetland plant material, 10 “decomposition bags” were inserted in the middle of each fertilization treatment of the STF experiment at the end of June 2003. The size of the bags was 5.5 x 6 cm made of 1 mm nylon mesh and filled with approximately 1.5 g of dried material (a natural mix of vascular plants and mosses). The incubating plant material had been collected from the living peat moss compartment from each block in 2002 and bags were filled with material come from the block where they were placed. All bags were inserted at the root level of vascular plants. The bags were collected after two incubating summer seasons (between August 5th and 14th 2004).

At the field camp, all bags were cleaned from external organic matter and rinsed with water to remove mineral material often deposited in the peat through time by strong winds of the Arctic. The material was air-dried for 48 h, oven-dried at 45°C for 24 h, and stored in polyethylene bags at field camp. Due to logistic constraint, the material was brought back to the laboratory at Laval University (Quebec City), re-dried at 45°C until constant weight, kept in desiccator and weighed to the nearest ± 0.001 g. Decomposition rates (DR) are expressed as percent of mass loss (Rocheffort *et al.* 1990):

$$DR = [(X_o - X) / X_o] * 100 \quad (3)$$

where X_o is the dry mass of the initial plant material and X is the dry mass of the plant material at the end of a growing season. Mean decomposition rates of the 10 bags were calculated for each experimental unit.

2.4.5 Chemical analyses

After two years of treatment application in all experimental units, total N and total P contents were analyzed in aboveground graminoid plants and mosses for both experiments. Total N and total P contents were also analyzed in organic matter from the decomposition bags for the STF experiment. Samples were pooled per category (graminoid plants, moss or litter) for each experimental unit before chemical analyses. Total N content was analysed

with a FIA (Quikchem 8000 of Lachat Instrument) and total P was measured with an ICP (model OPTIMA 4300DV of Perkin-Elmer) Procedures are described in Parkinson and Allen (1975). All chemical analyses were conducted at the Wood Science and Forest Department at Laval University (Quebec city).

2.4.6 Data analyses

To assess nutrient limitations and to estimate the fertilizing effect of geese on wetland arctic plants, two-ways ANOVAs for a complete randomized block design were performed, in the FTF experiment for aboveground primary production, cumulative leaf elongation, leaf counts per tiller, tiller and leaf densities, growth index for graminoid plants, productivity of mosses and total N and total P content in both graminoid plants and mosses. To test which type of nutrient limits growth in graminoids and mosses, each nutrient addition treatment was compared with the control (with plexiglas enclosure) using Dunnett's one-tailed a-priori test because our initial prediction was that nutrient addition should have a positive effect on plant growth. We conducted this test for each measured variable. A paired t-test was also used to compare both types of control (no nutrient addition treatment with or without a plexiglas enclosure).

In the case of STF experiment, aboveground primary production, tiller and inflorescence density and percentage cover of graminoid plants; primary production and percentage cover of mosses; decomposition rate and total N and total P contents of graminoid plants, mosses and organic matter in decomposition bags were analysed with two-ways ANOVAs for a complete randomized block design. To evaluate the effects of fertilization, we did 12 a-priori contrast tests to compare fertilizing treatment. First, we tested if fertilizing treatments had an effect on measured variables with one a-priori contrast test. We also compared the effect of faeces and glycin additions with their N equivalent ($1 \text{ g} / \text{m}^2$) with two a-priori contrast tests. Then, three a-priori contrast tests were done to test the effect of fertilizer combinations (same dose of N alone or with P, same dose of P alone or with N and two doses of a combination of two fertilisers). After, we evaluated the effect of fertilizers when a single dose was applied in one dose (a complete dose in 2003) or two split doses (~ half of the dose in 2003 and the rest in 2004) with two a-priori contrast tests (one for N and one

for P). Finally, to evaluate the effects of increasing doses of fertilizer on measured variables, four a-priori polynomial contrast tests were applied (N and P linear and quadratic effects). Regressions were also done to test the impact of mean tiller weight, tiller density or inflorescence density on primary production of graminoid plants.

For all analyses and experiments, level of significance was set to $p < 0.05$ and data were tested for homogeneity and normality and were transformed when necessary. Moss phosphorus content in the FTF experiment had to be rank transformed before analyses. All analyses were conducted using the general linear models procedure of SAS Software (2003).

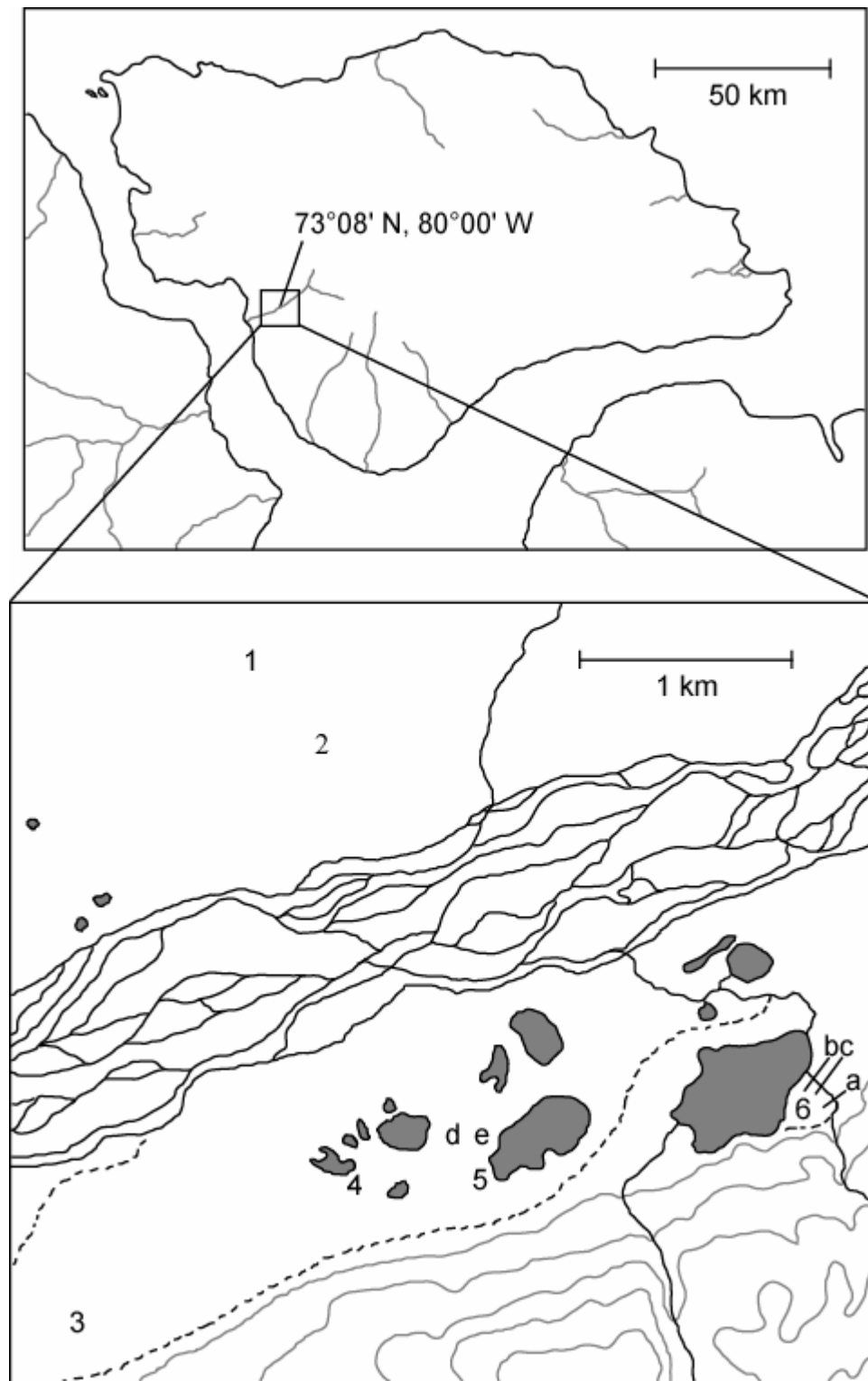


Figure 2.1 Location of study area in the Canadian Arctic, North of Baffin Island. Letters (a to e) represent blocks for the first trial fertilization (FTF) experiment and numbers (1 to 6) are blocks for second trial fertilization (STF) experiment.

Table 2.1 Mean percentage cover per species for control treatment after one growing season in the second trial fertilization (STF) experiment (n = 24). + = less than 0.5%.

Vascular plants	Cover	Bryophytes	Cover
Graminoids	~ 8.5	Brown mosses	~ 93.0
<i>Arctagrostis latifolia</i> R. Br.	+	<i>Aulacomnium palustre</i>	+
<i>Carex aquatilis</i> var <i>stans</i> Drej.	0.6	<i>Aulacomnium turgidum</i>	1.2
<i>Dupontia fisheri</i> R. Br.	6.0	<i>Brachythecium turgidum</i>	1.0
<i>Eriophorum scheuchzeri</i> Hoppe	1.9	<i>Bryum algovicum</i> var. <i>algovicum</i>	0.8
Non-graminoids	~ 0.5	<i>Bryum cryophilum</i>	+
<i>Cardamine pratensis</i> L.	+	<i>Calliargon giganteum</i>	+
<i>Pedicularis albolabiata</i> (Hultén) Kozh.	0.5	<i>Campylium stellatum</i> var. <i>arcticum</i>	1.9
<i>Ranunculus hyperboreus</i> Rottb.	+	<i>Cinclidium arcticum</i>	12.5
<i>Salix arctica</i> Pall.	+	<i>Drepanocladus</i> sp.	73.2
<i>Saxifraga cernua</i> L.	+	<i>Meesia triquetra</i>	1.2
<i>Stellaria longipes</i> Goldie	+	<i>Oncophorus wahlenbergii</i>	+
		<i>Polytrichum strictum</i>	0.7
		<i>Sphagnum</i> sp.	+
		Hepatics	+



Figure 2.2 Experimental unit used in the second trial fertilization (STF) experiment.

Table 2.2 Description of fertilizing treatments used in the FTF¹ experiment and in the STF² experiment.

FTF experiment		STF experiment		
Treatment	g m ⁻²	Treatment	g m ⁻²	Year(s) of application ³
1 - Control A (without enclosure)	-	1 - Control	-	-
2 - Control B (with enclosure)	-	2 - Faeces / m ²	40 ^a	2003 - 2004
3 - Faeces / m ²	40 ^a	3 - Glycin	2.5	2004
4 - Nitrogen (N)	1	4 - Nitrogen (N)	1	2003 - 2004
5 - N	10	5 - N	3	2003 - 2004
6 - Phosphorus (P)	0.6	6 - N	5	2003 - 2004
7 - P	3	7 - N	5	2003
8 - N + P	10 + 0.6	8 - N	15	2003
		9 - Phosphorus (P)	1	2003 - 2004
		10 - P	3	2003 - 2004
		11 - P	5	2003
		12 - N + P	3 + 0.5	2003 - 2004
		13 - N + P	5 + 1	2003 - 2004
		14 - N + P	15 + 2.5	2003

¹ FTF = First trial fertilization experiment

² STF = Second trial fertilization experiment

³ Treatments were applied during two years in the FTF experiment.

^a Number of faeces / m²

2.5 Results

2.5.1 Effect of enclosures

Among all the parameters measured in the FTF experiment, only moss production was higher in the control with an enclosure (control B; $50 \pm 8 \text{ g m}^{-2}$) than without confinement (control A; $26 \pm 3 \text{ g m}^{-2}$) ($t = 3.57$, $P = 0.038$; for all other comparisons, $P > 0.05$). To be constant with other treatments, we used data for control B only (with an enclosure).

2.5.2 Nutrient addition effects

2.5.2.1 Growth parameters of graminoid plants and mosses

Graminoid plants of tundra wetlands responded to nutrient addition treatments only when N was applied at doses equal or higher than 5 g of N / m^2 . These effects can first be seen on different plant growth parameters. High additions of N (10 g / m^2) had a significant positive effect on leaf and tiller densities of graminoid plants in the FTF experiment (Fig. 2.3). The same positive effect was observed for the highest dose of N (5 g / m^2) on tiller density in the STF experiment (significant linear effect for N, contrast 9 in Table 2.3 and Fig. 2.4). Tiller density in control treatment was lower than the average of nutrient additions ones (contrast 1 in Table 2.3). Significant positive linear effect of N was also found for the cover of graminoid plants but this effect was negative for mosses (contrast 9 in Table 2.3 and Fig. 2.5). At the end of 2004 growth season, graminoid plants covered 20 % and mosses 82 % in high N dose experimental units (5 g of N / m^2) compared to a cover of 8 % for graminoid plants and 94 % for mosses in control experimental units. Cover of graminoid plants in control treatment was higher than the average of nutrient additions ones (contrast 1 in Table 2.3). Additions of N had no effect on inflorescence density of graminoid plants in STF experiment (contrasts 9 and 10 in Table 2.3). Additions of P had no effect on growth parameters of graminoid plants and on cover of graminoid plants and mosses in both experiments (Fig 2.3 and 2.5; contrasts 11 and 12 in Table 2.3). Growth parameters and cover estimated in faeces and glycine treatments were not significantly different in the N equivalent treatment (1 g / m^2) (contrasts 2 and 3 in Table 2.3).

2.5.2.2 Primary production of graminoids plants and mosses

The higher growth of graminoid plants under N additions equal or higher than 5 g / m² translated into a significant higher aboveground primary production of graminoid plants (Fig. 2.6 and significant linear and quadratic effects of N; contrasts 9 and 10 in Table 2.3 and Fig. 2.7). Fifty-one % of the increase of aboveground graminoid plants production was explained by an increase of tiller density and 28 % by an increase in inflorescence density (Fig. 2.8). Nevertheless, the mean tiller weight did not explain the increase of vascular plants production. Additions of P had no effect on the aboveground primary production of graminoids in both experiments (Fig. 2.6 and contrasts 11 and 12 in Table 2.3).

Primary production of mosses was lower in control treatment than the average of nutrient addition ones in the STF experiment (contrast 1 in Table 2.3). However, moss production was not affected by nutrient additions (Fig 2.6 and contrasts 9 to 12 in Table 2.3) despite a trend for a higher production under N or P addition treatments compared to control in the FTF experiment (Fig. 2.6) and for all N additions in the STF experiment (Fig. 2.7). The no response of mosses to nutrient additions could originate from the considerable variance within treatments.

In addition, primary productions of graminoid plants and mosses estimated in faeces and glycin treatments were not significantly different in the N equivalent treatment (1 g / m²) (contrasts 2 and 3 in Table 2.3).

2.5.2.3 Decomposition rates

Contrary to the increased in growth and production caused by nutrient additions, decomposition rates were not significantly affected by nutrient additions (contrasts 9 to 12 in Table 2.4). Percentage of mass loss was 21.5 ± 0.8 % (mean \pm SE, n = 84) in our experimental units. Decomposition rates estimated in faeces and glycin treatments were not significantly different in the N equivalent treatment (1 g / m²) (contrasts 2 and 3 in Table 2.4).

2.5.2.4 Nutrient content

In the FTF experiment, total N and P content in graminoid plants under nutrient additions of 10 g of N / m² or 3 g of P / m² were significantly higher than control treatment (Fig. 2.9). On the opposite, N additions had no significant effect on total N content in graminoid plants in the STF experiment (contrasts 9 and 10 in Table 2.4 and Fig. 2.10). The same trend was observed for total P content; P additions had no significant effect on total P content (contrasts 11 and 12 in Table 2.4 and Fig. 2.10). Total P content was significantly lower under N addition of 5 g / m² (linear effect of N addition; contrast 9 in Table 2.4). The mean of total P content for control treatment was of 0.31 % compared to 0.23 % under N addition of 5 g / m², a diminution of 26 %. Total P content in control treatment was higher than the average of fertilizing ones (contrast 1 in Table 2.4).

In the FTF experiment, N content in mosses increased significantly following an addition of N equal or higher than 1 g / m². Under P additions equal or higher than 0.6 g / m², P content in mosses was higher than control treatment (Fig. 2.9). In the STF experiment, N and P contents were significantly higher under N addition of 5 g / m² (linear effect of N addition; contrast 9 in Table 2.4 and Fig. 2.10). The mean of nutrient contents for control treatment was 0.92 % of N and 0.11 % of P compared to 1.4 % of N and 0.41 % of P under 5 g of N / m², an increase of 56 and 282 %. Total P content was also significantly higher under P addition of 3 g / m² (linear effect of P addition; contrast 11 in Table 2.4 and Fig. 2.10). The mean of total P content for control treatment was 0.11 % compared to 0.41 % under 3 g of N / m², an increase of 273 %. In addition, total N and P contents in control treatment was lower than the average of fertilizing ones (contrast 1 in Table 2.4) and was higher in high NP treatment (3 g of N / m² + 0.5 g of P / m²) than in low NP treatment (5 g of N / m² + 1 g of P / m²) (contrast 6 in Table 2.4, data not shown).

In the STF experiment, total N content of organic matter in decomposition bags was significantly higher under N addition of 5 g / m² (linear effect of N addition; contrast 9 in Table 2.4 and Fig. 2.10). Total N content started at 0.60 % for control treatment to 0.70 % for a N addition of 5 g / m², an increase of 17 %. Total P content of organic matter was not affected by N or P addition (contrasts 9 to 12 in Table 2.4 and Fig 2.10).

In addition, total N and P content in graminoid plants, mosses and organic matter estimated in faeces and glycin treatments were not significantly different in the N equivalent treatment (1 g / m²) (contrasts 2 and 3 in Table 2.4).

2.5.2.5 Synergic effect of combined NP additions

High additions of N (10 g / m²) with P (with 0.6 g of P / m²) had a more pronounced positive effect on the leaf and tiller densities, index of growth and the primary production of graminoid plants than high additions of N (10 g / m²) or P (0.6 g of P / m²) alone in the FTF experiment (Fig. 2.4 and 2.6). The enhancement of biomass under nutrient additions was already present in the first year (1995; data not shown here, see Pineau 1999) but much stronger in the second year following fertilization (1996). For the NP additions treatment, which had the strongest effect on plant production, aboveground primary production of graminoid plants averaged 30 g / m² for the control units compared to 80 g / m² in the high N and P combination treatment units, at the end of the first year. This corresponds to an increase of 166 % for the biomass. Comparatively, biomass increased of 193 % after the second year (43 g / m² for the control vs 126 g / m² for the high N and P combination treatment, Fig. 2.6). No effect of NP additions was detected comparatively to N or P additions alone for moss production. In the STF experiment, moss production was higher when N was applied with P (contrast 4 in Table 2.3 and Fig. 2.11). There was a 55 % increase for the primary production in experimental units that received the smallest dose (3 g of N / m² and 0.5 g of P / m²) compared to the experimental units under N addition of 3 g / m² and a 21 % increase in experimental units that received the highest dose (5 g of N / m² and 1 g of P / m²) compared to the experimental units under N addition of 5 g / m². However, no effect of NP additions was detected comparatively at P additions for moss production (contrast 5 in Table 2.3). No effect of NP additions was detected comparatively to N or P additions alone for growth parameters and production of graminoid plant and for cover of mosses and graminoid plants (contrast 4 and 5 in Table 2.3).

In the FTF experiment, high additions of N (10 g / m²) with P (with 0.6 g of P / m²) had not a more pronounced positive effect on the total N or P content in graminoid plants and in mosses than high additions of N (10 g / m²) or P (3 g / m²) alone (Fig. 2.9). In the STF

experiment, total N content in organic matter in decomposition bags was smaller when N was applied with P (contrast 4 in Table 2.4 and Fig. 2.11). There was a diminution in N content of 7 % for the smaller dose (3 g of N / m² and 0.5 g of P / m² vs 3 g of N / m² alone) and of 21 % for the highest dose (5 g of N / m² and 1 g of P / m² vs 5 g of N / m² alone). Total P content of moss was higher when N was applied with P (contrast 4 in Table 2.4 and Fig. 2.11). There was an increase in N content of 46 % for the smaller dose (3 g of N / m² and 0.5 g of P / m² vs 3 g of N / m² alone) and of 107 % for the highest dose (5 g of N / m² and 1 g of P / m² vs 5 g of N / m² alone). Finally, total N content of moss was higher when P was applied with N (contrast 5 in Table 2.4, data not shown). There was an increase in N content of 45 % for the NP dose (5 g of N / m² and 1 g of P / m²) compared to P additions alone (5 g of N / m²). No effect of NP additions was detected comparatively to N or P additions alone for total N content of graminoid plant, total P content in graminoid plants and organic matter and decomposition rates (contrast 4 and 5 in Table 2.3). There was also no effect of NP additions comparatively at N additions alone for total N content in mosses (contrast 4 in Table 2.3). In addition, no effect of NP additions was detected compared to P additions alone for total P content in mosses and total N content in organic matter (contrast 5 in Table 2.3).

2.5.2.6 Effect of additions of a single dose vs a split dose over two years

In STF experiment, an application of N in one dose influenced significantly and positively tiller and inflorescence densities compared to an application in two split doses (contrast 7 in Table 2.3 and Fig. 2.12). Tiller and inflorescence densities were 1.6 and 5 times higher when N was applied in one dose compared to two split doses (3706 vs 2328 tiller / m² and 206 vs 44 inflorescence / m²). Then, total N content in graminoid plants and in mosses were lower when N was applied in one dose comparatively to two split doses (2.2 % vs 1.9 % for graminoid plants and 1.4 % vs 1.1 % for mosses) (contrast 7 in Table 2.4 and Fig. 2.12). Other variables were not significantly different when N was applied in one dose compared to an application in two split doses (contrast 7 in Tables 2.3 and 2.4).

Application of P in two split doses influenced significantly and positively primary production of mosses and decomposition rates in the STF experiment (contrast 8 in Tables

2.3 and 2.4). Primary production of mosses was 37 % higher when P was applied in two split doses compared to one dose. Decomposition rates increased of 22 % when P was applied in two split doses compared to one dose. However, total P content of mosses was 53 % lower when P was applied in two split doses comparatively to one dose (contrast 8 in Tables 2.4). Other variables were not significantly different when P was applied in one dose compared to an application in two spit doses (contrast 8 in Tables 2.3 and 2.4).

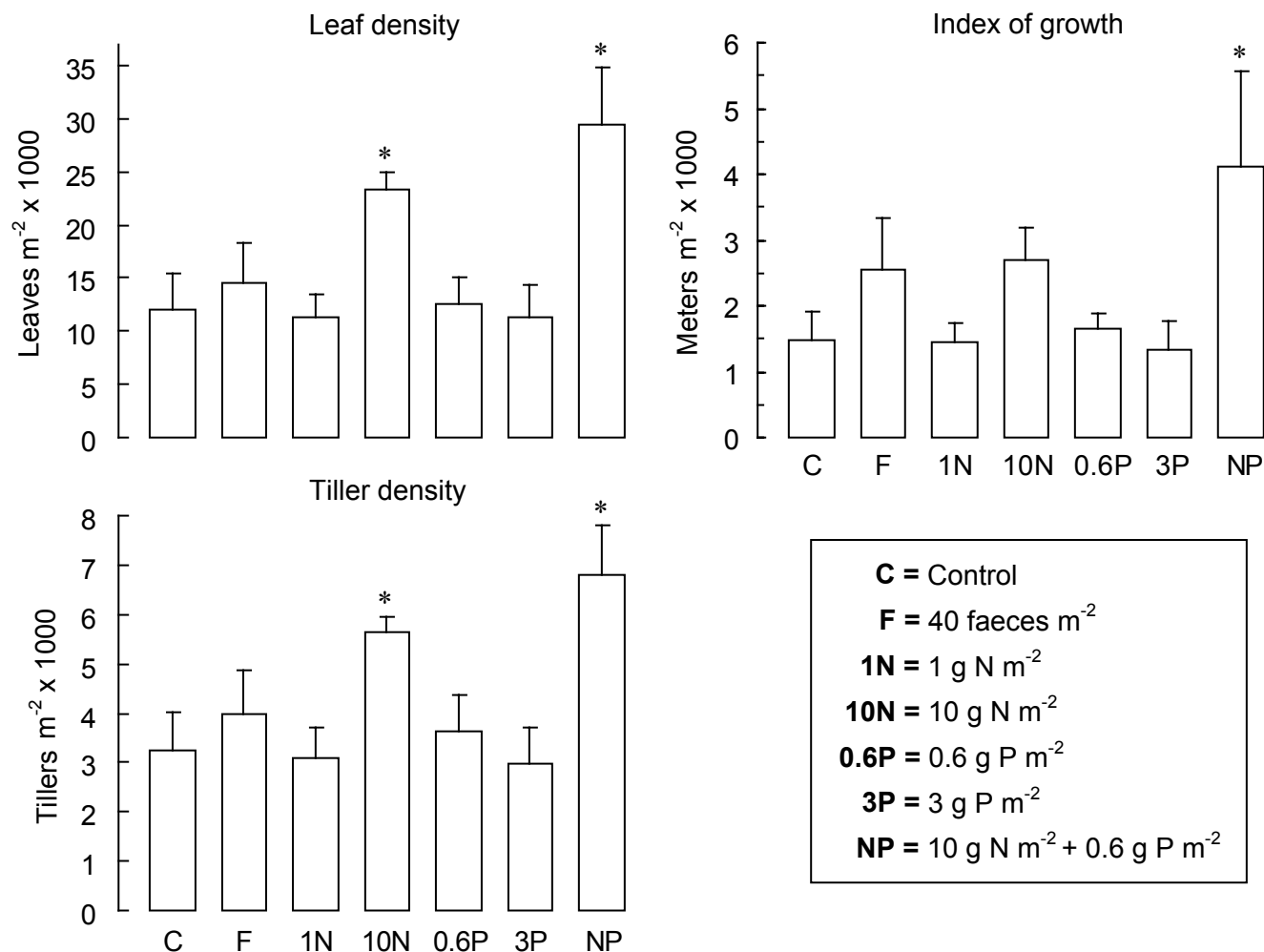


Figure 2.3 Effect of nutrient additions on leaf density, index of growth and tiller density of graminoid plants after one growing season in the first trial fertilization (FTF) experiment. Mean + SE ($n = 5$ for C, F, 1N, 0.6P and 3P treatments; $n = 4$ for 10N and NP treatments). * = Treatments significantly differ from the control at $P < 0.05$ (Dunnett's one-tailed test).

Table 2.3 Two-way ANOVAs and contrast multiple range a priori tests to evaluate the effects of nutrient additions on growth parameters of graminoids plants and mosses after two growing seasons in the second trial fertilization (STF) experiment. Numbers in parenthesis refer to treatments in Table 2.2. *P* values in bold emphasize significant differences.

Source of variation	Densities													
	Tiller			Inflorescence			Primary production			Cover percentage				
	Graminoid		P	Graminoid		P	Graminoid		P	Graminoid		P	Moss	
	d.f.	F _{18,65}		F _{18,65}		P	F _{18,65}		P	F _{18,65}		P	F _{18,65}	P
Block	5													
Treatment	13	3.71	<0.01	1.33	0.22		4.25	<0.01	3.30	<0.01	3.08	<0.01	1.84	0.06
Error	65													
Total	83													
Contrasts														
1) Control (1) vs Other treatments (2 to 14)	1	4.60	0.04	0.81	0.37		1.82	0.18	9.29	<0.01	9.06	<0.01	2.43	0.12
2) Faeces (2) vs 1N (4)	1	1.17	0.28	0.98	0.33		0.97	0.33	3.66	0.06	0.07	0.79	0.45	0.51
3) Glycine (3) vs 1N (4)	1	1.32	0.26	0.21	0.65		0.43	0.52	2.22	0.14	0.18	0.67	0.15	0.70
4) N (3,6,8) vs N + P (12,13,14)	1	0.10	0.75	3.40	0.07		1.15	0.29	6.61	0.01	1.68	0.20	3.40	0.07
5) P (9) vs P + N (13)	1	0.01	0.92	0.14	0.71		0.30	0.59	2.24	0.14	1.74	0.19	0.00	0.95
6) N + P (low) (12) vs N + P (high) (13)	1	0.31	0.58	3.61	0.06		0.32	0.58	1.30	0.26	0.30	0.59	0.03	0.86
7) 1 application N (7) vs 2 applications N (5)	1	5.44	0.02	4.86	0.03		2.16	0.15	0.01	0.94	0.12	0.73	2.37	0.13
8) 1 application P (11) vs 2 applications P (10)	1	0.03	0.86	0.01	0.94		0.10	0.76	4.55	0.04	0.04	0.84	0.09	0.76
9) Nitrogen linear effect	1	9.45	<0.01	1.43	0.24		16.90	<0.01	2.39	0.13	16.23	<0.01	6.72	0.01
10) Nitrogen quadratic effect	1	2.78	0.10	2.41	0.13		5.58	0.02	1.15	0.29	0.06	0.81	1.95	0.17
11) Phosphorus linear effect	1	0.62	0.43	0.38	0.54		0.03	0.87	0.63	0.43	0.93	0.34	0.02	0.90
12) Phosphorus quadratic effect	1	0.40	0.53	1.53	0.22		0.04	0.85	2.56	0.12	0.92	0.34	0.66	0.42

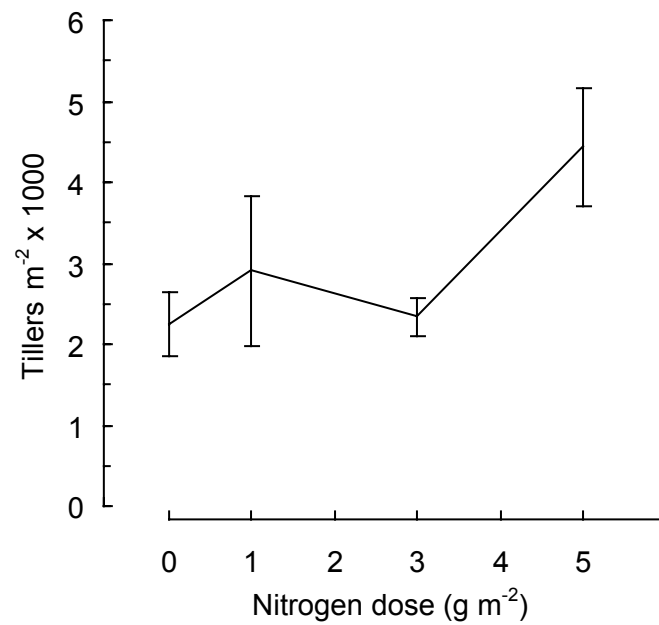


Figure 2.4 Effect of nutrient additions of tiller density of graminoid plants after two growing seasons in the second trial fertilization (STF) experiment. Mean \pm SE (n = 6). Linear effect of nitrogen is significant. See Table 2.3 for *P* values.

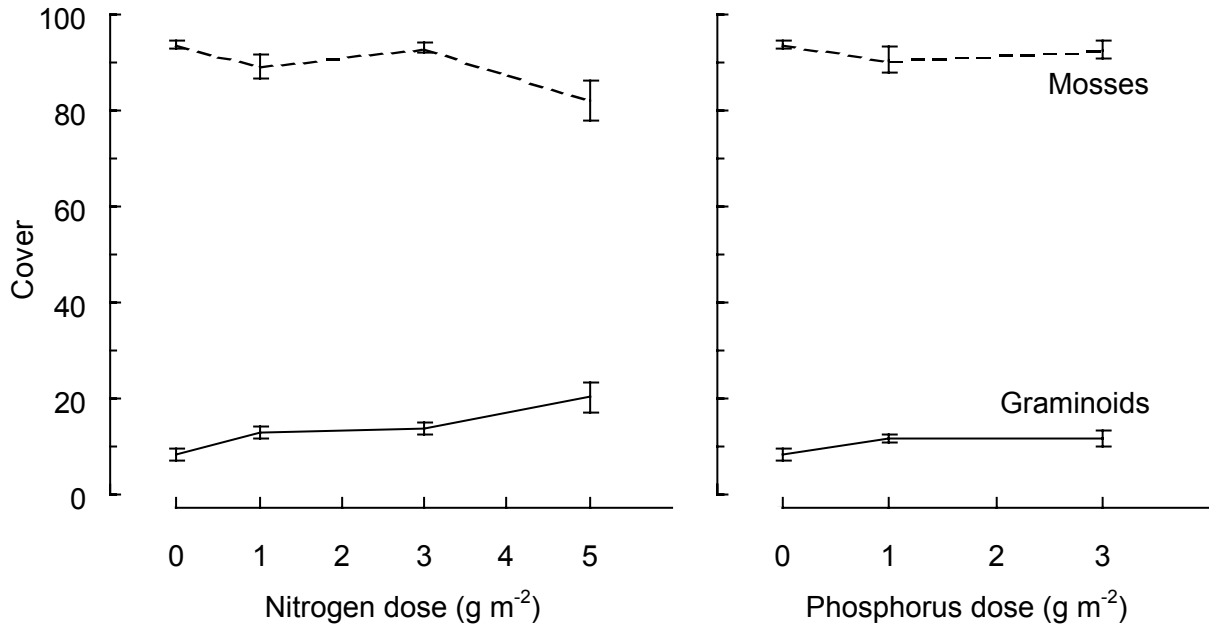


Figure 2.5 Effect of nitrogen and phosphorus additions on percentage cover of graminoid plants and mosses after two growing seasons in the second trial fertilization (STF) experiment. Mean \pm SE ($n = 6$). Linear effect of nitrogen is significant for graminoids and mosses. See Table 2.3 for P values.

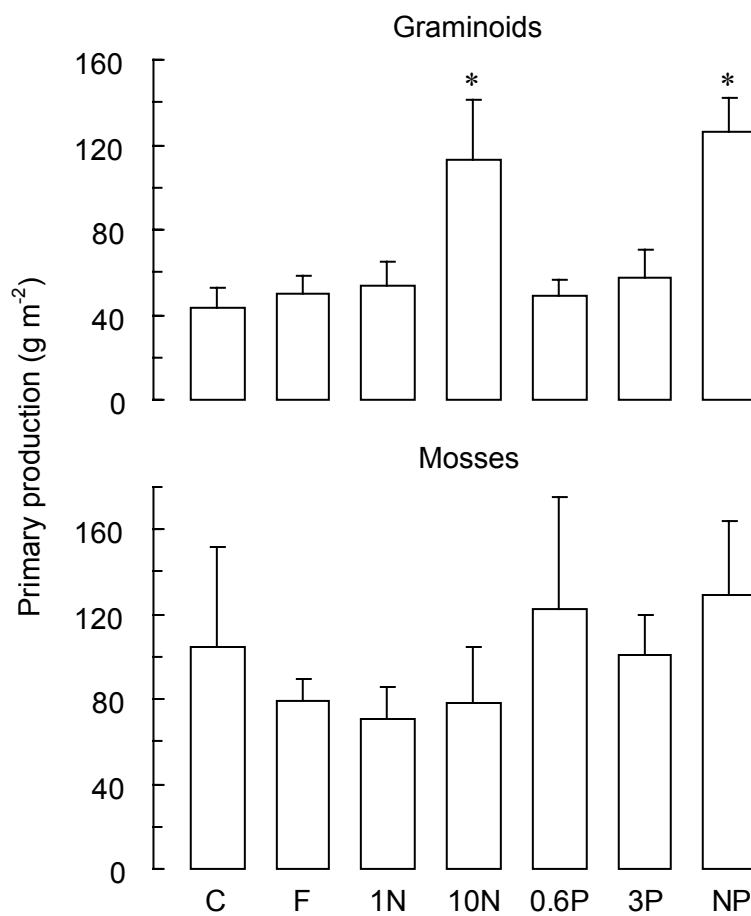


Figure 2.6 Effect of nutrient additions on primary production of graminoid plants and mosses after two growing season in the first trial fertilization (FTF) experiment. Mean + SE (n = 5 for graminoid plants and n = 3 for mosses). See Figure 2.3 for treatment description. * = Treatments significantly differ from the control at $P < 0.05$.

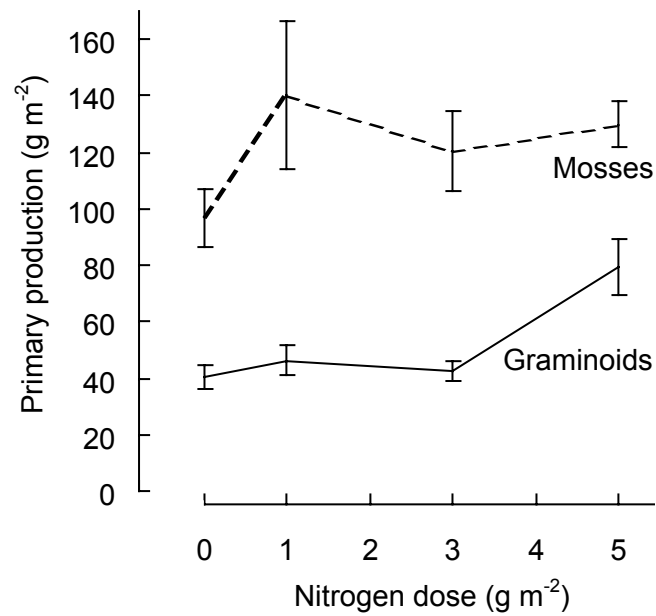


Figure 2.7 Effect of nitrogen additions on primary productivity of graminoid plants and mosses after two growing seasons in the second trial fertilization (STF) experiment. Mean \pm SE ($n = 6$, except for treatment 0 g/m^2 for moss PP, $n = 5$ and for treatments 3 and 5 g/m^2 for moss PP, $n = 4$). Linear and quadratic effects of nitrogen are significant for graminoid plants. See Table 2.3 for P values.

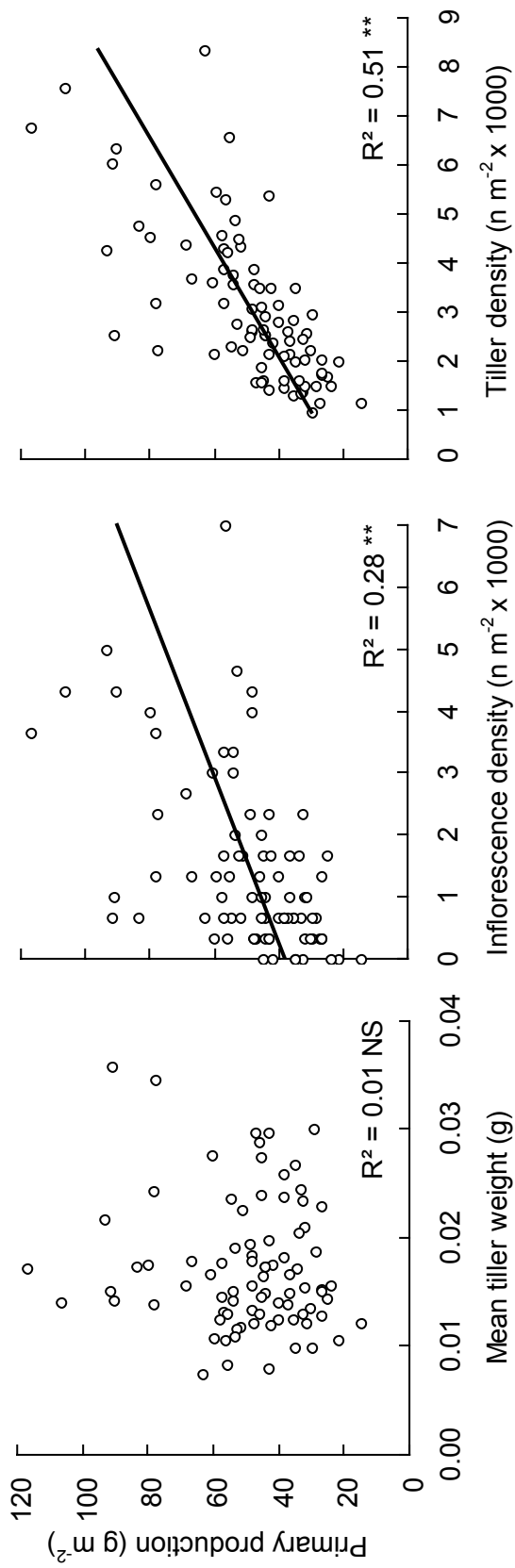


Figure 2.8 Relation between primary production of graminoid plants and mean tiller weight, tiller density and inflorescence density after two growing seasons in the second trial fertilization (STF) experiment (n = 84). ** = Significant regression at $P < 0.01$, NS = not significant.

Table 2.4 Two-way ANOVAs and contrast multiple range a priori tests to evaluate the effects of nutrient additions on total nitrogen content and total phosphorus content of graminoid plants, mosses and organic matter in decomposition bags and on decomposition rates (DR) after two growing seasons in the second trial fertilization (STF) experiment. Numbers in parenthesis refer to treatment in Table 2.2. *P* values in bold emphasize significant difference.

Source of variation	Total nitrogen content						Total phosphorus content								
	Graminoid		Moss		Organic matter		Graminoid		Moss		Organic matter		DR		
	d.f.	F _{18,65}	P	F _{18,65}	P	F _{18,65}	P	F _{18,65}	P	F _{18,65}	P	F _{18,65}	P		
Block	5														
Treatment	13	1.28	0.25	7.26	< 0.01	1.47	0.15	3.21	< 0.01	38.25	< 0.01	0.65	0.80	0.85	0.61
Error	65														
Total	83														
Contrast															
1) Control (1) vs Other treatments (2 to 14)	1	0.43	0.51	15.77	< 0.01	0.29	0.59	5.15	0.03	17.19	< 0.01	0.02	0.90	0.04	0.84
2) Faeces (2) vs 1N (4)	1	3.16	0.08	1.36	0.25	1.70	0.20	3.61	0.06	1.33	0.25	0.06	0.81	2.55	0.12
3) Glycine (3) vs 1N (4)	1	0.25	0.62	0.00	1	0.31	0.58	0.15	0.70	0.06	0.8	0.01	0.92	1.76	0.19
4) N (3,6,8) vs N + P (12,13,14)	1	0.70	0.41	0.01	0.92	7.38	< 0.01	1.88	0.18	38.55	< 0.01	0.23	0.63	0.28	0.60
5) P (9) vs P + N (13)	1	2.48	0.12	24.36	< 0.01	0.00	0.99	2.43	0.12	0.47	0.49	0.82	0.37	0.61	0.44
6) N + P (low) (12) vs N + P (high) (13)	1	0.14	0.71	8.19	< 0.01	0.72	0.40	0.77	0.38	12.19	< 0.01	0.02	0.90	0.00	0.99
7) 1 application N (7) vs 2 applications N (5)	1	4.65	0.04	0.50	0.75	0.16	0.70	0.07	0.79	0.04	0.84	1.60	0.21	0.01	0.94
8) 1 application P (11) vs 2 applications P (10)	1	0.45	0.50	0.10	0.75	2.76	0.10	0.19	0.66	46.64	< 0.01	1.79	0.19	4.07	0.05
9) Nitrogen linear effect	1	2.04	0.16	39.96	< 0.01	5.89	0.02	10.38	< 0.01	0.00	0.96	0.01	0.91	0.46	0.50
10) Nitrogen quadratic effect	1	0.04	0.84	1.47	0.23	2.25	0.14	0.66	0.42	0.09	0.76	0.00	0.95	0.24	0.62
11) Phosphorus linear effect	1	1.25	0.27	8.88	< 0.01	1.08	0.30	0.01	0.93	213.81	< 0.01	0.83	0.37	1.38	0.24
12) Phosphorus quadratic effect	1	1.41	0.24	0.55	0.46	0.03	0.87	1.25	0.27	2.19	0.14	0.01	0.94	0.26	0.61

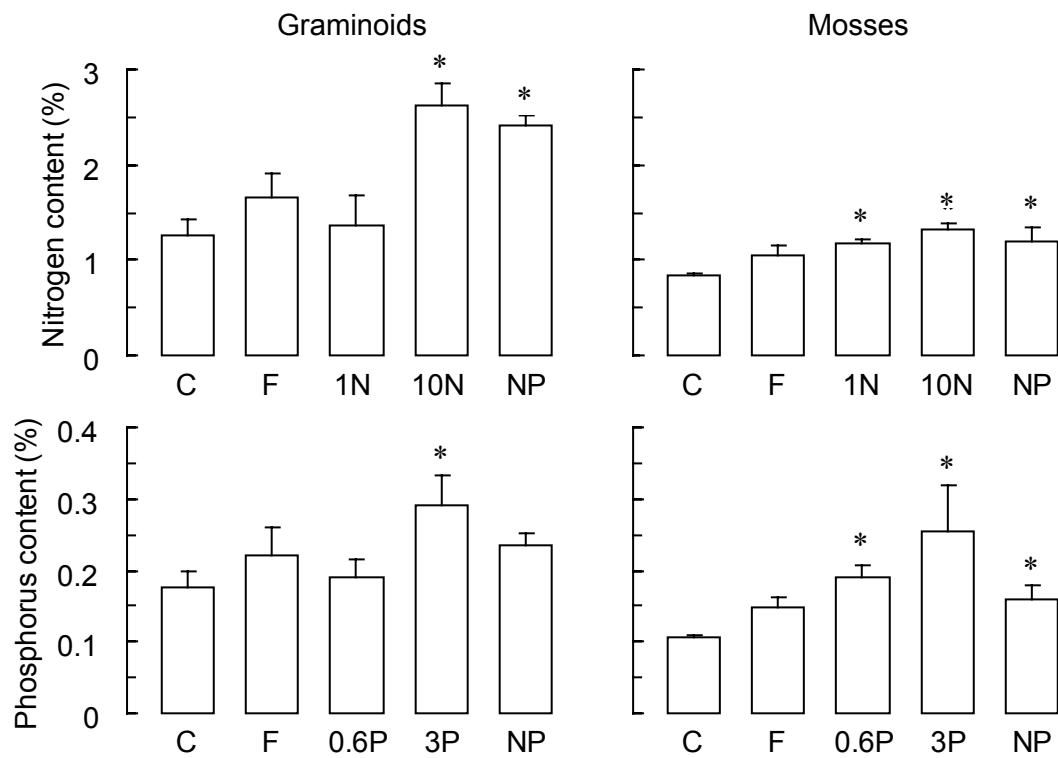


Figure 2.9 Effect of nutrient addition on nitrogen and phosphorus contents for graminoid plants and mosses after two growing seasons in the first trial fertilization (FTF) experiment. Mean + SE (n = 4). See Figure 2.3 for treatment description. * = Treatments significantly differ from the control at $P < 0.05$ (Dunnett's one-tailed tests).

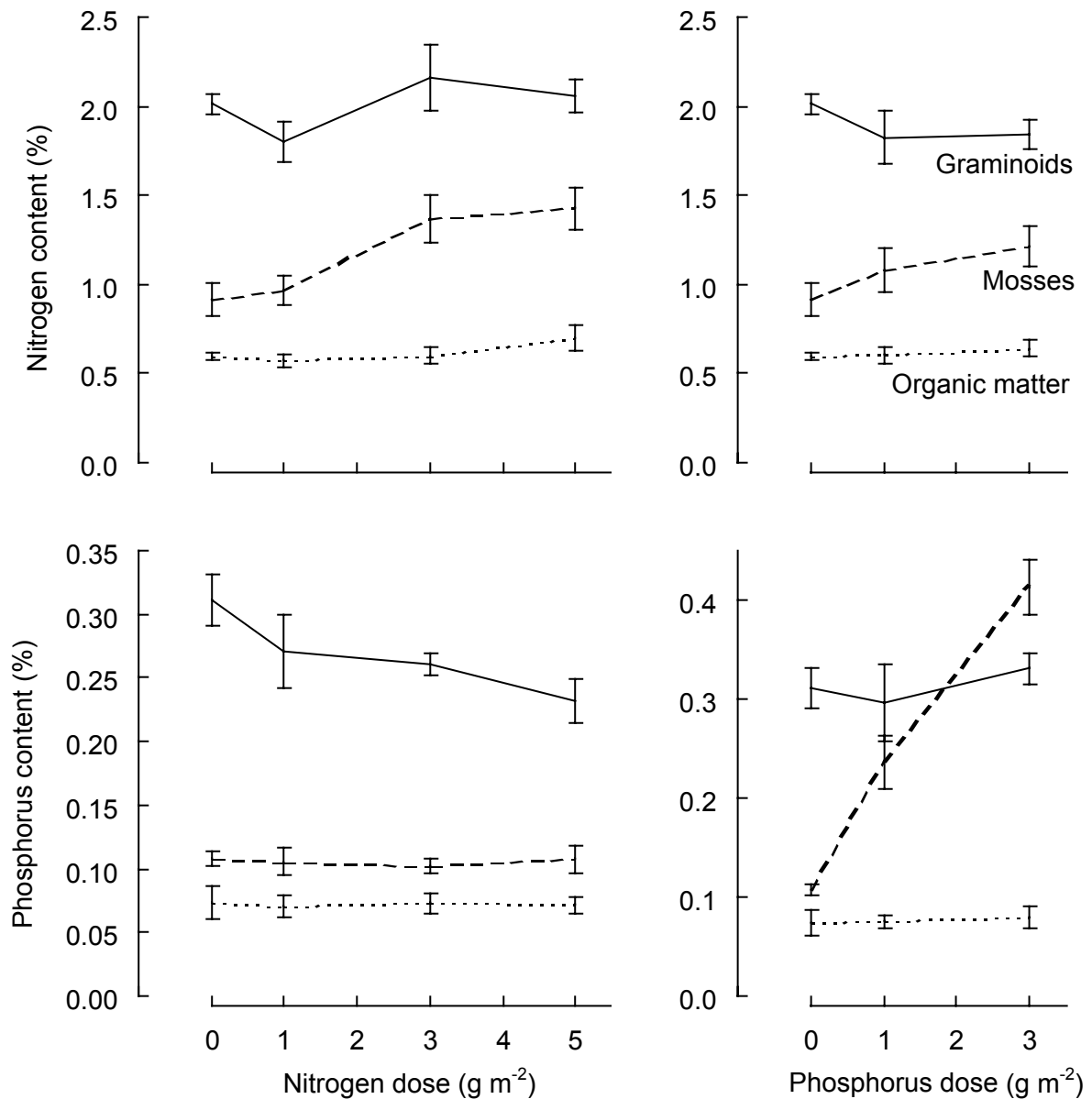


Figure 2.10 Effect of nitrogen and phosphorus additions on nitrogen and phosphorus contents of graminoid plants, mosses and organic matter in decomposition bags after two growing seasons in the second trial fertilization (STF) experiment. Mean \pm SE ($n = 6$). Linear effect of nitrogen for N content of mosses and organic matter and for P content of graminoid plants are significant. Linear effect of phosphorus for N content of mosses and for P content of mosses are significant. See Table 2.4 for P values.

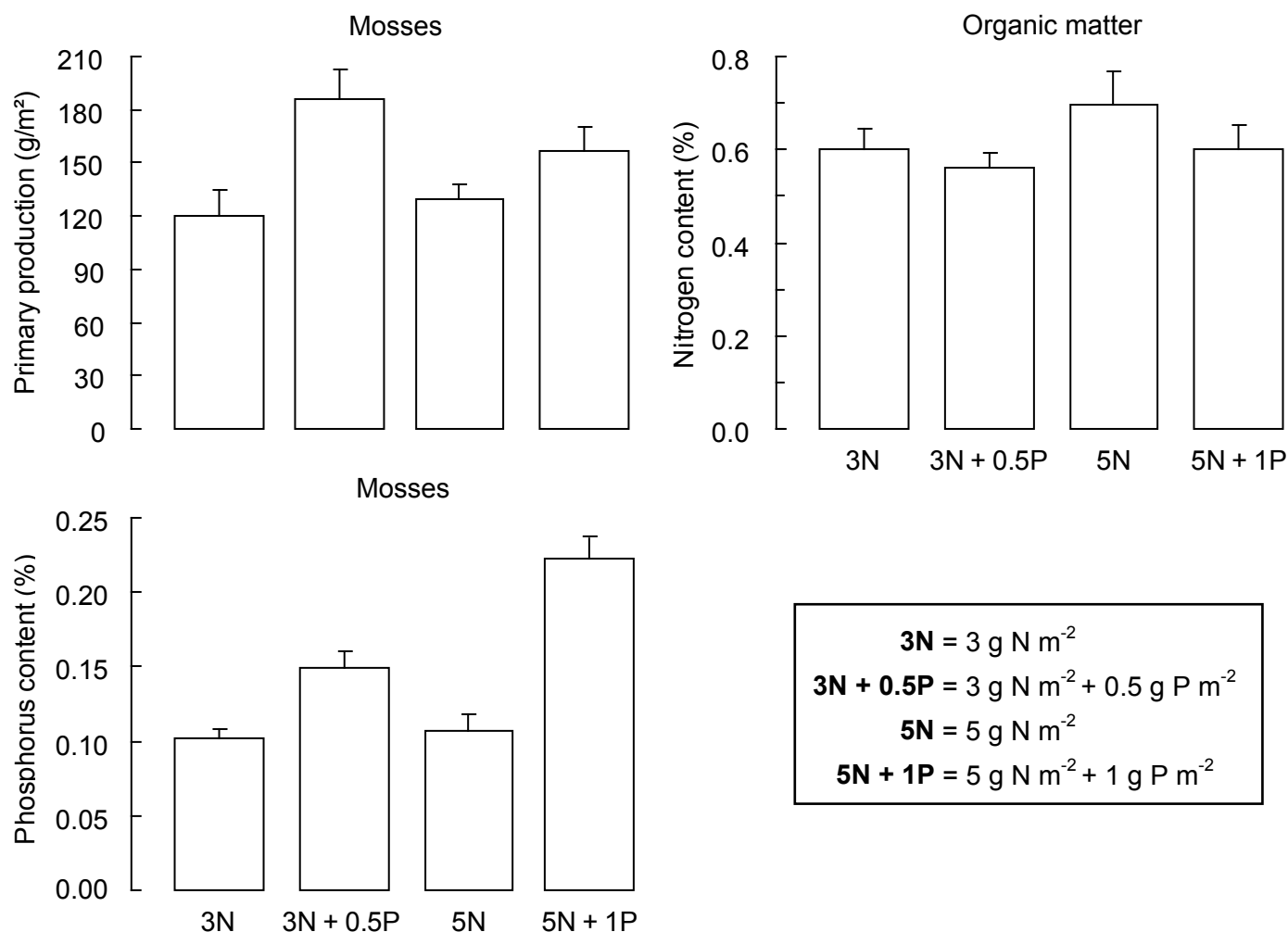


Figure 2.11 Effect of nitrogen additions on primary production and phosphorus content of mosses and on nitrogen content of organic matter in decomposition bags when N was applied alone or in combination with P after two growing seasons in the second trial fertilization (STF) experiment. Mean + SE (n = 6, except for treatment 3N + 0.5P for moss primary production where n = 5 and for treatments 3N and 5N for moss primary production where n = 4). All comparisons are significant, see Tables 2.3 and 2.4 for *P* values.

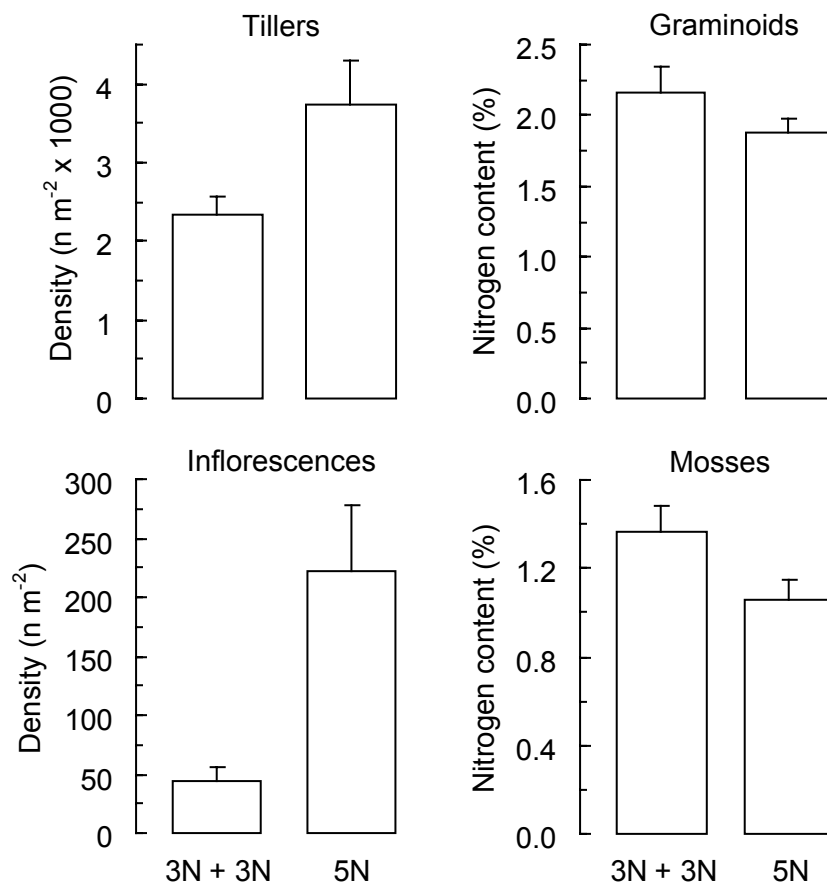


Figure 2.12 Effect of nitrogen additions on tiller and inflorescence densities and on nitrogen content of graminoid plants and mosses after two growing seasons in the second trial fertilization (STF) experiment when fertilizer was applied in one dose (2003) or in two split doses (2003 and 2004). Mean + SE ($n = 6$). Treatment codes: 3N + 3N = 3 g / m² N in 2003 + 3 g / m² N in 2004, 5N = 5 g / m² N in 2003 + 0 g / m² N in 2004. All comparisons are significant, see Tables 2.3 and 2.4 for P values.

2.6 Discussion

2.6.1 Justification of enclosure designs

Enclosures used in the FTF experiment had no effect on the growth of vascular plants but improved moss production. As mosses are poikilohydric, they only grow when they are wet on the surface as they have no roots to draw water. One explanation for the higher moss production in the control with plexiglas enclosure is the accumulation of water in the enclosure after rainfalls because water could not seep out (Pineau, personal observation). Even though we observed moss growth differences between the two controls, our results should not be affected because all treatments were in plexiglas enclosures and consequently microclimate conditions were uniform. The rationale for using plexiglas enclosures in the FTF experiment was to control leaching of nutrient additions. On the other hand, potential long-term effects (improvement of moss growth and reduction of graminoid plant production) of this kind of enclosure and results of the FTF experiment guided the experimental approach of the STF experiment. To avoid water retention, enclosures were done with chicken wire fences.

2.6.2 Nutrient limitation in Polygon fens

Based on the N : P ratio of water samples taken from each block of the STF experiment (ratios < 9 for five blocks and < 12 for the one block, R. Pouliot, unpublished data), polygon fens were N-limited on Bylot Island. In fact, an N:P ratio inferior to 10 corresponds to a N-limited system, between 10 and 20 to a co-limited, N-limited or P-limited system and superior to 20 to a P-limited system (Güsewell 2004). Then, we suspected that graminoid plants and bryophytes are also N-limited in the tundra wetlands of Bylot Island. To confirm this suspicion, effects of nutrient additions on growth parameters of graminoid plants and mosses were studied.

2.6.2.1 Graminoid Plants

As predicted from the N:P ratio found in water samples of the experimental sites, both trials showed that N was the most limiting nutrient for the growth of graminoid plants in the

tundra polygon fens of Bylot Island. Leaf density, index of growth, tiller density, cover percentage and primary production were all positively influenced by N additions (higher or equal than 5 g / m²) alone and in combination with P. Even if some growth variables were promoted by an N + P additions, P alone had no impact on them. Then, it seems that graminoid plants in polygon fens are not P-limited on Bylot Island. The aboveground phytomass increase to N addition was better explained by an increase of tiller or inflorescence density than by an increase of tiller weight. It appears that graminoid plants invested more in rhizomes for creating new tillers than in existing tillers when they received additional loads of nitrogen. In the Arctic, the rhizome system of graminoid plants is generally well developed, representing more than 90 % of the total plant biomass. For example, belowground biomass of graminoid plants in Bylot Island polygon fens are 322 g / m² comparatively at 30 g / m² for their aboveground biomass (Pineau 1999). At the end of a growing season, we believed that nutrients are efficiently translocated into rhizomes and plants benefit from these nutrient resources the next spring for producing new tillers and therefore increasing tiller density.

Nitrogen limitations have been found for some studies in arctic wet ecosystems (e.g. Haag 1974; McKendrick *et al.* 1978; Shaver & Chapin 1995; Gough and Hobbie 2003) where nitrogen addition had a positive effect on aboveground phytomas, leaf mass per tiller or cover of graminoid plants. Nevertheless, Shaver and Chapin (1995) have also observed a phosphorus positive effect on leaf mass per tiller in wet sedge tundra. They concluded that the type of nutrient limitation is related to site characteristics. In our study site, wind transport of sediment could explain why polygon fens were not P-limited since erosion is an important source of phosphorus for all ecosystems (Chapin *et al.* 1978). The relative importance of short-term and long-term responses of vegetation must also be taking into consideration when analysing the effects of nutrient additions (Chapin *et al.* 1995). According to Chapin (1980), nutrients absorbed in one year have often their most pronounced effect upon growth and reproduction in subsequent years. Studies of Shaver and Chapin (1995) or Gough and Hobbie (2003) clearly demonstrated that growth variables responded more efficiently to fertilization after two or more years. The same trends were observed in the FTF experiment: there was an increase of 166 % after on year, but of 193 % after the second year for the above ground phytomass under a high N + P nutrient additions,

the most efficient treatment. The response of arctic plants to nutrient additions appears to be variable and we propose that this is due to variability in soil type, site, number of years with fertilization, lap of time between fertilization and variable measurements and tested doses.

Are graminoid plants of arctic polygon fens able to uptake amino acids from the soil and incorporated these directly in their structures, as proposed by Kielland (1997) and Henry & Jefferies (2003b)? The amino acids could correspond up to the half of the nitrogen uptaken by plants in arctic environment (Kielland 1997). However, we have not found glycine addition effect on any measured variable for graminoid plant growth. After one year of glycine application, glycine treatment had the same effect than the 1 g / m² of N addition. We originally suspected that glycine treatment would have a higher effect than 1 g / m² of N treatment because we believed that plants would be able to uptake the majority of the added 2.5 g / m² of glycine. It is well known that vegetation responses to nutrient additions are often expressed two or more years after the first addition (Chapin 1980). We suggest longer monitoring time before drawing any conclusion on the response of tundra wetland plants from glycine fertilisation.

2.6.2.2 Mosses

In contrast to graminoid plants and the N:P ratio found in water samples of the experimental sites, both trials showed that N was not the most limiting nutrient for the growth of mosses in the tundra polygon fens of Bylot Island. Even though moss nutrient concentrations were higher for both N and P additions, moss production was little affected by treatments in the FTF experiment. In the STF experiment, no effect was detected for nitrogen or phosphorus addition alone despite a trend for higher values with nutrient additions equal or higher than 1 g / m². However, nitrogen content in mosses was higher with nitrogen addition and phosphorus content was higher with phosphorus addition. Furthermore, bryophytes accumulated more phosphorus in their tissues under N + P additions comparatively with N additions alone and more nitrogen under P + N additions when we compare with P additions alone. All these observations showed that nitrogen and phosphorus were not a limiting nutrient because they accumulated in tissues rather than

promoted the moss growth. Bryophyte growth was probably limited by other factors like water, temperature or other nutrient.

Only few studies estimated fertilization effects on bryophytes growth in arctic environment (Jónsdóttir *et al.* 1995; Gordon *et al.* 2001), none in wet polygons, then, it is difficult to compare our results with other studies. In a N fertilization experiment in Iceland, on a well-drained, post-glacial lava field, growth and shoot density of bryophytes tended to be higher after a N addition (total of three years of N additions: 1.2 g / m²) (Jónsdóttir *et al.* 1995). For Gordon *et al.* (2001), on a heath on Svalbard, N and P moss concentrations were higher after nutrient additions. However, bryophyte cover was two times higher after phosphorus addition (5 g / m²) whereas nitrogen addition (1 or 5 g / m²) did not influence their cover. They concluded that bryophytes were P-limited on this habitat. Like for graminoid plants, nutrient limitations are probably highly related to soil and site characteristics.

2.6.3 Nutrient additions from geese

It appears that vascular plants were and mosses tended to be N-limited in Bylot Island polygon fens. Thus, what are the nutrient addition effects of goose droppings? Even if aboveground primary production of vascular plants was not promoted by faeces additions or its N equivalent additions (1 g / m²), there was a positive trend for bryophytes production. Furthermore, N additions equal or higher than 5 g / m² had a positive impact of graminoid production whereas P additions between 0.6 and 3 g / m² had no effect. However, N faeces equivalent additions promoted the nutrient concentration for bryophytes but not for vascular plants in both trials. Then, we proposed that fertilizing effect of geese is especially caused by N. Even if this effect was low when we considered average droppings in the polygon fens of the Island (17.4 faeces / m² = ~ 0.44 g of N / m²), it could become very important on a small scale. Areas with well-developed graminoid plant communities and a high density of ponds constituted preferred habitats for grazing activities (Hughes *et al.* 1994). Large groups of geese often grazed on a particular patch of polygon fens up to exhausting their food. They also relaxed in group on a small area. Then, the amount of droppings was higher in these areas and the fertilizing effect of geese was probably much greater than the one observed by faeces treatment or their N equivalent. In

addition, we observed that when graminoid plants were protected from grazing, their cover was higher under N additions whereas bryophytes cover was lower. This phenomenon was observed in many studies (e.g. Graglia *et al.* 2001; Granberg *et al.* 2001; Grellmann 2002; Pauli *et al.* 2002, Gough & Hobbie 2003; Bret-Harte *et al.* 2004). Graminoid plants improved their growth, which then increase their cover. In turn, the shade created by the larger graminoid covers impacted bryophytes growth. Under grazing pressure, goose droppings probably do not promote the abundance of graminoid plants. However, they could favour their regrowth by adding important amounts of nutrients.

Goose droppings also added P in polygon fens. Despite of this, no effect of P was observed on graminoid plant or moss growth. Nevertheless, this nutrient could play a role in the fertilizing effect of geese in that ecosystem. Güsewell *et al.* (2002) propose that there was a positive effect of P additions on the availability of N. P improves N acquisition and retention in plants on floating fens (Güsewell *et al.* 2003). The same effect was observed in arctic polygon fens: when we added N with P, N content of organic matter in decomposition bags dropped. More N was uptaken by plants, as showed by an increase of primary production of bryophytes. It was also observed that P fertilization experimental units have intercepted more atmospheric N than others (Lamers *et al.* 2000). A possible explanation is that P additions was rapidly immobilized and subsequently released slowly when plants needed an additional input of P to maintain their growth (van der Hoek *et al.* 2004). That could compensate for the possible shift in nutrient limitation when N was added alone, as suggested by Güsewell *et al.* (2002; 2003). Then, P present in goose faeces probably helped the growth or regrowth of graminoid plants in polygon fens, but the effect was indirect via few processes that have promoted the uptake and assimilation of N.

Even if goose faeces supply important amounts of nutrients easily available for grazed graminoid plants in polygon fens of Bylot Island, we needed to add nutrients in quantities greater than those provided to this ecosystem by the current goose population to see any answer. Based of 2004 goose population estimation, geese deposited approximately 0.44 g of N / m² per year by their faeces and growth of graminoid plants was increased only after additions of 5 g of N / m². What could explain this phenomenon? We think that moss layer could be a good way for the interpretation of this difference.

2.6.5 Moss constrain in trophic interactions between mosses, graminoid plants and geese

In our study, under N additions of 1 g / m², the moss carpet acted like a natural barrier, by sequestering most added nutrients and by preventing their absorption by the roots of graminoid plants. With an increase of the nitrogen dose, bryophytes have absorbed more and more N without increasing their production up to their saturation point, as showed in Fig. 2.5 and 2.8. Under N additions of 5 g / m², the absorption capacity of mosses had probably been exceeded, allowing the nutrient surplus to seep through to the roots of graminoid plants. Then, nitrogen content of organic litter increased and consequently more N was available for graminoid plants. As a consequence, aboveground primary production and tiller density of graminoid plants were higher at 5 g / m² of N. This could explain why tiller and inflorescence densities were higher and N content was lower when nitrogen was added in one time (complete dose in 2003) rather than in two times (~ half of the dose in 2003 and the other half in 2004). When N was applied in two split doses, bryophytes sequestered the entire N added but when N was applied in one dose, they became saturated in nitrogen and vascular plants improved their growth with the remaining N. The N content was lower in vascular plants when N was applied in one time because a dilution effect was created. The quantity of N was diluted in a higher graminoid plant production when N was applied in one time. Our results are consistent with other studies in moss dominated habitats where no effect on graminoid plant growth was found when N concentrations used were less than 10 g / m² (e.g. Henry *et al.* 1986; Pineau 1999).

So, can the moss barrier hypothesis explained the discrepancy of the vegetation response observed from fertilization experiments conducted in arctic wetlands over the last 30 years? In fact, contrary to the positive effect of faeces reported by Bazely and Jefferies (1985) in Manitoba, studies carried out on Bylot Island the mossy polygon wetlands expressed no increase neither in the biomass nor in the nitrogen concentration of graminoid plant tissues after faeces additions (Beaulieu *et al.* 1996, Pineau 1999, this study; Table 2.5). One explanation for the absence of responses on Bylot Island could be linked to the faeces density. Likewise, a low dropping density (1.8 faeces / m²) proves insufficient to promote growth of plants in Alaskan salt marshes (Zacheis *et al.* 2002ab) On Bylot Island, the

faeces density in 2004 was about 17.4 faeces / m². Is this faeces density insufficient to promote growth of grazed graminoid plants? We believe that the absent of graminoid plant increase of growth are more likely to be explained by the presence of a moss layer in freshwater wetlands. Compared to the mineral soil found in the tidal flats, mosses restrict the uptake of mineralized nitrogen from the faeces by sequestering the nutrients first (Kotanen 2002). Then, the results are not contradictory, but depend on the presence or not of a moss carpet or a deep humus layer. Henry *et al.* (1986) show that graminoid plant species have only a little response to fertilization in their wet sedge meadow experimental site. The response is intermediate at their site dominated by *Cassiope tetragona* (L.) D. Don where a thin organic layer was present (0 to 5 cm). However, graminoid plants and forbs of their mesic site dominated by *Dryas integrifolia* Vahl. with no developed organic layer showed positive increased standing crop to all their fertilization treatments (N ranging from 1 to 9.75 g / m² and P ranging from 1 to 5 g / m²). This study supports our general assessment of how graminoid plants respond to fertilization in tundra wetlands in relation with moss layer even though that true replicates are only two with no spatial dispersion in the landscape. It was difficult to find some trend in fertilization studies that took place in tundra wetlands with a dominant mossy ground layer or a well developed organic soil for several reasons. First, a very high dose of fertilizer was often applied with no intermediate treatment. Secondly, fertilizers were applied in combination like N+P or N+P+K, but not alone, and then conclusions for a particular nutrient are not possible. Nevertheless, according to a literature review (Table 2.5), the graminoid plants showed an increased growth or a greater N and P tissue contents only under certain conditions. For N, it appears that the application of fertilizer has to be equal or greater than 5 g / m² when N was applied alone. Haag (1974) observed a positive answer with only one dose of 3.4 g / m², but he had only two nearby replicates (1.5 m between the replicates). For P, the fertilizer dose needs to be higher than 3 g / m² when P was applied alone. It is 11.5 and 115 times higher for N and P respectively than the nutrients brought by the faeces of the population of geese in 2004. On the opposite, our study showed that bryophytes responded at N additions equal or higher than 1 g / m² by showing a positive response for N content and a positive trend for production. Then, our hypothesis was confirmed: bryophytes benefit more than graminoid

plants from a sudden pulse of nutrients coming from the deposition of goose faeces (moss carpet hypothesis, Gauthier *et al.* 1996; Pineau 1999; Kotanen 2002).

The constraining action from the moss layer, which was already described but not tested in other publications of our laboratory (Beaulieu *et al.* 1996; Gauthier *et al.* 1996; Kotanen 2002) and briefly suggested by Shaver & Chapin (1995), as being most likely a major factor controlling tundra plant responses to nutrient additions. This study confirmed that constraining action. ^{15}N experiments in tussock tundra in northern Alaska showed immediate moss uptake following application and a steady decrease in absorption over time, while vascular plants showed a steady uptake of ^{15}N throughout the two months of the experiment, mostly from N weakly adsorbed by the brown moss compartment (Marion *et al.* 1982). Kotanen (2002) showed that bryophytes absorbed the majority of ^{15}N when it was added at the soil surface, whereas graminoid plants absorbed more ^{15}N than bryophytes when it was applied below the surface. In a natural grazed system such as Bylot Island, faeces density and timing both play a role in the vegetation response. Because of the low level of nutrient additions coming from goose faeces in our system, it may take more than two years to the nutrients to become available to the graminoid plants (Beaulieu 1995) or the level of fertilization from goose faeces may be too low to have any detectable effect on the vegetation. Effects of N additions on decomposition rates and nitrogen content of organic litter in decomposition bags measured at the vascular root level confirm that hypothesis. As shown in our study, no effect was detected in decomposition rates or nitrogen content of organic matter. Even at a N addition of $5 \text{ g} / \text{m}^2$, added nitrogen was all sequestered either by bryophytes or, when they became saturated, by graminoid plant roots. Jonasson *et al.* (1999) showed that soil microbial biomass absorbs extra nutrients only when uptake of nutrients by plants declines. In our case, the nitrogen content of litter showed a little increase but it is insufficient to promote microbial activity as demonstrated by a constant decomposition rate for all nitrogen doses. Then, the nutrient sink strength in plants was still active. The moss layer is efficient for blocking the nutrient access to the graminoid plants but also to the decomposer microorganisms.

Moss constrain in the recycling of nutrients can also explain the undercompensatory growth of grazed plants of Bylot Island, as suggested by Gauthier *et al.* (1995). As suggested by

McNaughton (1979; 1983), herbivore effects on plant fitness can be explained by three constraining views. First, herbivory is always detrimental to the grazed plants (diminution of fitness). Secondly, grazed plants can compensate for herbivory by using nutrients in their reserve organs (maintenance of fitness until some level of herbivory who leads to a fitness reduction). Finally, grazed plants can overcompensate due to intrinsic or extrinsic consequences of herbivory (increase of fitness until some level of herbivory who leads to a fitness reduction). Organic wastes of herbivores can help grazed plants to compensate for grazing (McNaughton 1997). So, by what way do herbivory affect grazed plants on polygon fens? Grazed graminoid plants are able to develop new tillers after grazing by geese, but graminoid plant production never reaches biomass levels obtain by the same species when they are not grazed. Two reasons could explain the undercompensatory growth: grazing occurs too late in the season when the regrowth capacity of graminoid plants is low or the moss carpet sequestrated nutrients releases from goose faeces for a long period. Our study seems to promote the second reason. A particular grazed patch of graminoid plants on polygon fens have to scoop out their resources to regrowth after grazing. However, nutrients available in reserve organs seem to be insufficient to have a true compensatory growth. Grazed plants could need additional input of nutrients to maintain their fitness at the same level that when they are not grazed. The natural input of nutrient in polygon fens come from goose faeces and are probably not immediately available to graminoid plants. To conclude, graminoid plant fitness was reduced but this was not due to a detrimental effect or herbivory but to a nutrient sequestration by mosses.

In addition, turnover of nutrient is not really promoted by faeces addition in polygon fens with a dense moss carpet as on Bylot Island. Even if bryophytes productivity tended to be higher when faeces were added, they sequester nutrients for many years. Then, no change in graminoid plant nutrient availability was observed in these short-term nutrient addition experiments.

Table 2.5 Results of nutrient addition experiments on graminoid plants in tundra wetlands with a dominant mossy ground layer or a well developed organic soil. Only papers that clearly described the studied habitat were considered. Site of Bazely and Jefferies (1985) study have no mossy ground layer or a well developed organic soil but it is included for faeces treatments comparisons.

Author(s), habitat(s) and study site(s)	Parameters measured after <i>t</i> growing season	Graminoid plants	Treatments ^a					
			N	P	NP	NPK	Faeces	Faeces
Bazely & Jefferies (1985) ¹	Production (<i>t</i> = 1)	<i>Puccinellia phryganodes</i> , <i>Carex subspathacea</i>	•	•	•	•	•	+
Tidal flats; (n = 5)	N content (<i>t</i> = 1)	Idem	•	•	•	•	•	+
La Pérouse Bay, Manitoba								
Beaulieu <i>et al.</i> (1996) ²	Production (<i>t</i> = 1)	<i>DuPontia fisheri</i> , <i>Eriophorum scheuchzeri</i>	•	•	•	•	•	ns
Low center polygon fens; (n = 4)	N content (<i>t</i> = 1)	Idem	•	•	•	•	•	ns
Bylot Island, Nunavut								
Chapin <i>et al.</i> (1975) ^{3,4}	Production (<i>t</i> = 1) ³	<i>D. fisheri</i> , <i>Eriophorum angustifolium</i> , <i>Carex aquatilis</i>	•	•	•	•	ns	•
Low center polygon fens; (n = 2)	Production (<i>t</i> = 1) ⁴	Idem	•	•	•	•	+	•
Barrow, Alaska	N content (<i>t</i> = 1) ^{3,4}	Idem	•	•	•	•	ns	•
	P content (<i>t</i> = 1) ^{3,4}	Idem	•	•	•	•	+	•
Gough & Hobbie (2003) ⁵	Production (<i>t</i> = 4)	All graminoid plants	+	ns	+	•	•	•
Moist non-acidic tundra; (n = 3)	Cover (<i>t</i> = 4)	Idem	+	ns	+	•	•	•
Toolik Lake, Alaska								

^a • = no data; ns = no significant effect; + = positive effect; - = negative effect.

¹ Positive response for either treatments of circa 100, 300 or 575 g/m².

² Faeces added 3 times throughout the growing season by grazing goslings in experimental enclosures.

³ Treatment = 9 g/m² of N + 4.5 g/m² of P + 7.2 g/m² of K.

⁴ Treatment = 3.6 g/m² of N + 14.4 g/m² of P + 4.5 g/m² of K.

⁵ Treatment N = 10 g/m²; treatment P = 5 g/m²; treatment NP = 10 g/m² of N + 5 g/m² of P.

Table 2.5 (suite) Results of nutrient addition experiments on graminoid plants in tundra wetlands with a dominant mossy ground layer or a well developed organic soil. Only papers that clearly described the studied habitat were considered. Site of Bazely and Jefferies (1985) study have no mossy ground layer or a well developed organic soil but it is included for faeces treatments comparisons.

Author(s), habitat(s) and study site(s)	Parameters measured after <i>t</i> growing season	Graminoid plants	Treatments ^a					
			N	P	NP	NPK	Faeces	Faeces
Haag (1974) ⁶ Low center polygon fens; (n = 2)	Production (<i>t</i> = 1)	<i>Carex rariflora</i> , <i>Carex chordorrhiza</i> , <i>E. scheuchzeri</i> , <i>E. angustifolium</i>	+	-	+	•	•	•
Tuktoyaktuk, Northwest Territories								
Henry <i>et al.</i> (1986) ⁷ ⁸	Production (<i>t</i> = 3) ⁷	<i>Carex membranacea</i> , <i>E. angustifolium</i>	ns	•	•	•	ns	•
Wet sedge meadow; (n = 2)	Production (<i>t</i> = 3) ⁸	<i>C. membranacea</i>	ns	•	•	•	+	•
Alexandra fjord, Nunavut								
Mack <i>et al.</i> (2004) ⁹	Production (<i>t</i> = 20)	Vascular plants	•	•	+	•	•	•
Moist acidic tundra; (n = 4)	N content (shoot) (<i>t</i> = 20)	Idem	•	•	+	•	•	•
Toolik Lake, Alaska	N content (root) (<i>t</i> = 20)	Idem	•	•	+	•	•	•
McKendrick <i>et al.</i> (1978) ¹⁰	Leaf mass / tiller (<i>t</i> = 1)	<i>DuPontia fisheri</i>	+	ns	+	•	•	•
Tundra moist site; (n = 1)	N content (<i>t</i> = 1)	Idem	+	ns	+	•	•	•
Footprint Creek, Alaska	P content (<i>t</i> = 1)	Idem	ns	+	+	•	•	•

^a • = no data; ns = no significant effect; + = positive effect; - = negative effect.

⁶ Treatment N = 3.4 g/m²; treatment P = 2 g/m²; treatment NP = 3.4 g/m² of N + 2 g/m² of P.

⁷ Treatment N = 1.95 g/m²; treatment NP = 1 g/m² of N + 1 g/m² of P + 1 g/m² of K; aboveground phytomass for green parts only.

⁸ Treatment N = 9.75 g/m²; treatment NP = 5 g/m² of N + 5 g/m² of P + 5 g/m² of K; aboveground phytomass for green parts only.

⁹ Treatment = 10 g/m² of N + 5 g/m² of P.

¹⁰ Treatment N = 20.7 g/m²; treatment P = 14.7 g/m²; treatment NP = 20.7 g/m² of N + 14.7 g/m² of P.

Table 2.5 (suite) Results of nutrient addition experiments on graminoid plants in tundra wetlands with a dominant mossy ground layer or a well developed organic soil. Only papers that clearly described the studied habitat were considered. Site of Bazely and Jefferies (1985) study have no mossy ground layer or a well developed organic soil but it is included for faeces treatments comparisons.

Author(s), habitat(s) and study site(s)	Parameters measured after <i>t</i> growing season	Graminoid plants	Treatments ^a				
			N	P	NP	NPK	Faeces
Øien (2004) ¹¹	Production (site 1 and 2) (<i>t</i> = 2)	All graminoid plants	ns	ns	ns	•	•
Rich fen; (n = 3)	Production (site 3) (<i>t</i> = 2)	Idem	ns	ns	+	•	•
Sølendet Nature Reserve, Norway	Tiller density (site 1 and 2) (<i>t</i> = 2)	Idem	ns	ns	ns	•	•
	Tiller density (site 3) (<i>t</i> = 2)	Idem	ns	ns	+	•	•
Shaver & Chapin (1995) ¹²	Leaf mass / tiller (<i>t</i> = 2, 3, 4)	<i>E. angustifolium</i> , <i>C. aquatilis</i>	+	ns	ns	•	•
Wet sedge tundra; (n = 4)	N content (<i>t</i> = 2)	Idem	+	•	ns	•	•
Atigun River, Alaska	P content (<i>t</i> = 2)	Idem	•	+	+	•	•
Shaver & Chapin (1995) ¹²	Leaf mass / tiller (<i>t</i> = 3)	<i>E. angustifolium</i>	+	+	+	•	•
Wet sedge tundra; (n = 4)	Leaf mass / tiller (<i>t</i> = 2, 3, 4)	<i>C. aquatilis</i>	ns	+	+	•	•
Franklin Bluffs, Alaska	N content (<i>t</i> = 2)	Idem	+	•	ns	•	•
	P content (<i>t</i> = 2)	Idem	•	+	+	•	•
Shaver & Chapin (1995) ¹²	Leaf mass / tiller (<i>t</i> = 1)	<i>E. angustifolium</i>	ns	ns	ns	•	•
Wet sedge tundra; (n = 4)	Leaf mass / tiller (<i>t</i> = 2, 3, 4)	Idem	ns	+	+	•	•
Slope Mountain, Alaska							
Shaver & Chapin (1995) ¹²	Leaf mass / tiller (<i>t</i> = 1)	<i>E. angustifolium</i>	ns	ns	ns	•	•
Wet sedge tundra; (n = 4)	Leaf mass / tiller (<i>t</i> = 2, 3, 4)	Idem	+	+	+	•	•
Pump 2, Alaska	N content (<i>t</i> = 2)	Idem	ns	•	ns	•	•
	P content (<i>t</i> = 2)	Idem	•	+	+	•	•

^a • = no data; ns = no significant effect; + = positive effect; - = negative effect.

¹¹ Treatment N = 12 g/m²; treatment P = 3 g/m²; treatment NP = 12 g/m² of N + 3 g/m² of P.

¹² Treatment N = 25 g/m²; treatment P = 25 g/m²; treatment NP = 25 g/m² of N + 25 g/m² of P.

Table 2.5 (suite) Results of nutrient addition experiments on graminoid plants in tundra wetlands with a dominant mossy ground layer or a well developed organic soil. Only papers that clearly described the studied habitat were considered. Site of Bazely and Jefferies (1985) study have no mossy ground layer or a well developed organic soil but it is included for faeces treatments comparisons.

Author(s), habitat(s) and study site(s)	Parameters measured after <i>t</i> growing season	Graminoid plants	Treatments ^a				
			N	P	NP	NPK	Faeces
van Heerwaarden <i>et al.</i> (2003) ¹³	N content (<i>t</i> = 4)	<i>Eriophorum vaginatum</i>	+	•	•	•	•
Ombrotrophic part of the bog (n = 8)	P content (<i>t</i> = 4)	Idem	-	•	•	•	•
Stordalen, Sweden							
This study (1995-1996) ¹⁴							
Low center polygon fens; (n = 5)	Production (<i>t</i> = 2)	<i>C. aquatilis</i> , <i>D. fisheri</i> , <i>E. scheuchzeri</i>	+	ns	+	•	ns
Bylot Island, Nunavut	Leaves density (<i>t</i> = 1)	Idem	+	ns	+	•	ns
	Index of growth (<i>t</i> = 1)	Idem	ns	ns	+	•	ns
	Stem density (<i>t</i> = 1)	Idem	+	ns	+	•	ns
	N content (<i>t</i> = 2)	Idem	+	•	+	•	ns
	P content (<i>t</i> = 2)	Idem	•	+	ns	•	ns
This study (2003-2004) ¹⁵							
Low center polygon fens; (n = 6)	Production (<i>t</i> = 2)	<i>D. fisheri</i> , <i>E. scheuchzeri</i>	+	ns	ns	•	ns
Bylot Island, Nunavut	Stem density (<i>t</i> = 2)	<i>C. aquatilis</i> , <i>D. fisheri</i> , <i>E. scheuchzeri</i>	+	ns	ns	•	ns
	Inflorescence density (<i>t</i> = 2)	<i>C. aquatilis</i> , <i>D. fisheri</i> , <i>E. scheuchzeri</i>	ns	ns	ns	•	ns
	Cover (<i>t</i> = 2)	<i>C. aquatilis</i> , <i>D. fisheri</i> , <i>E. scheuchzeri</i>	+	ns	ns	•	ns
	N content (<i>t</i> = 2)	<i>D. fisheri</i> , <i>E. scheuchzeri</i>	+	ns	ns	•	ns
	P content (<i>t</i> = 2)	<i>D. fisheri</i> , <i>E. scheuchzeri</i>	+	ns	ns	•	ns

^a • = no data; ns = no significant effect; + = positive effect; - = negative effect.

¹³ Treatment = 10 g/m² of N.

¹⁴ Treatment N = 10 g/m²; treatment P = 3 g/m²; treatment NP = 10 g/m² of N + 0.6 g/m² of P; treatment faeces = circa 500 g/m²; treatments of 1 g/m² of N and 0.6 g/m² of P were also tested but induced no response.

¹⁵ Treatment N = 5 g/m²; treatment P = 3 g/m²; treatments NP = 3 g/m² of N + 0.5 g/m² of P and 5 g/m² of N + 1 g/m² of P; treatment faeces = circa 500 g/m²; treatments of 1 and 3 g/m² of N and 1 g/m² of P were also tested but induced no response.

2.7 Summary

On Bylot Island, vascular plants in polygon fens are N-limited, whereas bryophytes are not limited neither by nitrogen nor phosphorus. It was showed that the two-way trophic interaction between geese and grazed graminoid plants is more complex in wetlands with a dense carpet of bryophytes than in wetlands without or with few bryophytes. Thus, the role of bryophytes is very important in the polygon fens of Bylot Island. They modify the two-way trophic interaction in a three-way trophic interaction (Fig. 2.13) where they sequester the nutrients added by goose faeces and have an indirect negative effect on grazed plants. Svensson (1995) suggested that mosses could act as a small-scale autogenic ecological engineer by capturing nutrients early in their ecosystem fluxes and they could retain and relocate them within themselves, thereby counter-acting the potential spread of vascular plants. In fact, geese had a negative grazing impact on their preferred graminoid plants (Gauthier *et al.* 1995; 1996), but their faeces can not help the regrowth of these plant, as is generally the case in other environments (e.g. Bazely and Jefferies 1985). The faeces promote rather the productivity of bryophytes. Eventually, nutrients would be slowly released from the moss layer compartment through decomposition below the living moss carpet and gradually transferred to the roots of the graminoid plants at a steady rate but much later, as suggested in other moss dominated communities (Marion *et al.* 1982; Li and Vitt 1997). Further experiments are needed to explore the long-term fertilizing effects of goose droppings on bryophytes and graminoid plant productions, decomposition rates and nutrient turnover in arctic polygon fens.

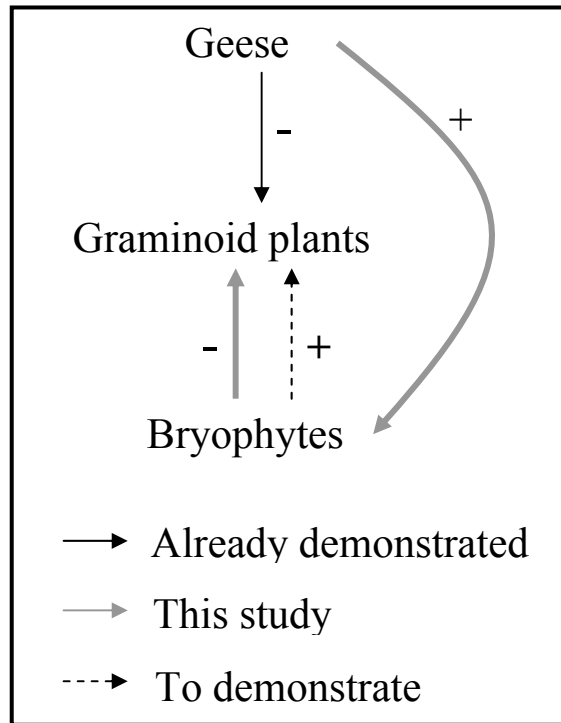


Figure 2.13 Graphic representation of trophic relations between the Greater snow geese, their preferred grazed plants and the bryophyte layer in polygon fens on Bylot Island.

Chapitre 3

Estimating stem elongation of brown mosses in arctic condition: comparison of three methods.

Rémy Pouliot, Line Rochefort & Gilles Gauthier

3.1 Résumé

Les méthodes pour estimer l'élongation des tiges de mousses en Arctique doivent considérer les réalités abiotiques et biotiques présentes dans le milieu et tenir compte des restrictions techniques propres aux régions isolées. Trois méthodes ont été testées durant cette étude. 1) Les tiges coudées sont à éviter car les perturbations de surface sont fréquentes en Arctique, créant ainsi des biais dans les calibrages. 2) Les marques permanentes blanches permettent le marquage des espèces proportionnellement à leur abondance. Cette méthode peut également s'adapter à diverses conditions abiotiques. Des valeurs probantes sont garanties en contrepartie d'une bonne préparation. 3) Les marqueurs naturels, malgré leur faible abondance relative, sont représentatifs de la production réelle des mousses. Cette méthode, de manipulation aisée, est appropriée pour estimer la production saisonnière sous une variété de conditions climatiques sans calibrage préalable, en autant que les marqueurs naturels soient relativement fréquents et bien dispersés. Dans les environnements où les coûts d'échantillonnage sont élevés et où les déplacements sont difficiles, il s'agit du meilleur choix.

3.2 Abstract

The methods chosen to estimate moss elongation in the Arctic must take abiotic and biotic realities into account. Technical restrictions of isolated regions have also to be taking into consideration. This study compared three methods used in tundra wetlands. 1) Cranked wires should be avoided mainly because surface disturbances are current events in Arctic. Thus, biases in calibration are created. 2) White permanent marks have the advantage to allow the marking of species proportionally to their abundance. This method can be also adaptable at many abiotic conditions. Accurate values are expected with an adequate preparation. 3) Innate markers, despite their low relative abundance, are representative of real moss production. That method, with easy manipulations, is appropriate to estimate seasonal production under many climatic conditions without prior calibration if innate marker species are relatively frequent and well dispersed. For environments where sampling costs are high and traveling is difficult, it is the most appropriate technique.

3.3 Introduction

Bryophytes are an important component of arctic ecosystems in terms of primary production, phytomass and species diversity, and are often the dominant plant group, especially in wet habitats like tundra polygon fens (Vitt & Pakarinen 1977; Russell 1990; Ellis & Rochefort 2004). Hence, growth of mosses becomes a key parameter to estimate when studying ecosystem processes in these environments. Techniques used to evaluate bryophyte stem elongation can be classified into two categories: biomass or harvest techniques and gas exchange technique (Russell 1988). In vulnerable ecosystems, like arctic environments, direct biomass harvesting techniques are judged not appropriate because sampling areas will take more time to recover after disturbance comparatively at temperate or tropical ecosystems. Indirect methods are recommended and frequently used in arctic environments. Cranked wires (Clymo 1970), tied threads (Tallis 1959) and fluorescent spray (Russell 1984), three indirect methods, are recommended by the International Tundra Experiment (ITEX) to estimate bryophyte stem elongation in arctic ecosystems (Jónsdóttir *et al.*, 1997) but we question their efficiency. Another study from our laboratory (Poulin 1995) compared three methods of bryophyte increment measurement: cranked wires (Clymo 1970), fluorescent spray (Russell 1984) and plastic bands (Lindholm 1990) on the growth of *Sphagnum* in southern peatlands and revealed that there were important differences between estimates. So, it is necessary to identify a method that can give true estimates of moss stem elongation and that can be used in any environment or climatic conditions to facilitate comparisons among sites and studies and this, particularly for the small brown mosses.

However, principal characteristics of arctic ecosystems are that, relative to temperate ones, they exhibit a low annual net primary production and individual moss stems composing the tundra communities are small, fragile and delicate (Haag 1974; Muc 1977). Since growing seasons are very short in these ecosystems (e.g. 50 days on Truelove Lowland, Devon Island in Nunavut (Muc 1977)), a short outstanding period could be determinant for the seasonal growth of bryophytes. Setting up experiments in those environments should be quick and early in the season because there is a risk to miss a large part of the annual

growth. Furthermore, some bryophytes are able of photosynthetic activity under the snow (e.g., *Drepanocladus uncinatus*, Collins & Callaghan (1980) or *Polytrichum sexangulare*, Lösch *et al.* (1983)) or immediately after removal of snow cover (*Kiaeria starkei*, Woolgrove & Woodin (1996)). It is probable that the same phenomenon occurs frequently in many ecosystems, in the Arctic or elsewhere. Thus, methods able to capture whole seasonal increments, from the snowmelt to the end of the growing season will be an advantage. Also, when foreign materiel is inserted into the moss carpet, the presence of permafrost and the frequence of surface disturbances (inundations and frost heaving) are important considerations when a specific method has to be chosen. Moreover, working in remote arctic regions can bring several constraints as one can reach a particular field site. For example, it can be needed to rent a helicopter or a plane and it is necessary to plan very well all movements. To conclude, the method chosen to estimate moss stem increments in these ecosystems must take the abiotic, biotic and logistic realities into account.

Two different fertilization studies done on Bylot Island are used to assess methods to estimate bryophyte stem elongation in the Arctic growing conditions. The aims were 1) to test a spray method (hereafter named the white mark technique) already used to estimate *Sphagnum* growth but not tested on smaller brown mosses in Arctic conditions, 2) to compare the white mark technique with the cranked wires and innate marker methods already used in that environment and 3) to suggest the best method to use when considering constraints from ecosystem or working conditions.

3.4 Methods

To compare the methods used to estimate moss stem elongation, we compiled data from different nutrient addition experiments conducted in the High Arctic between 1996 and 2004 in tundra polygon fens. The general goals of these studies were, in 1996, to determine limiting nutrients for plant growth (Pineau 1999) and in 2004, to evaluate the fertilizing effects of goose droppings on plant growth (c.f. chapitre 2). Discussion on the effects of the different treatments is not the focused of the present article, so only the methodological approach is examined. Methods used to estimate moss increments were cranked wires (1996), innate markers (1996 and 2004) and white marks (2004). The 1996 experiment will be refer to as the CW-I experiment (for comparison between cranked wires and innate markers) and the 2004 experiment as the WM-I experiment (for comparison between white marks and innate markers). Moss nomenclature is done according to Anderson *et al.* (1990).

3.4.1 Study area

The studies were carried out in a glacial valley (70 km²) located on the southwest plain of Bylot Island, Nunavut, Canada (73°08' N - 80°00' W). Lowlands are characterised by wet tundra polygons, typically ranging from 10 to 20 m in diameter. Most of them are concaves and form freshwater fens or shallow ponds. Fens and pond margins are covered by graminoids such as *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe and *Carex aquatilis* var *stans* Drej. growing through a dense and continuous carpet of mosses dominated by *Drepanocladus* sp. (mainly *D. revolvens*).

The moss layer was surveyed with estimations of percent cover of each species at mid-August 2004 in four quadrats (25 cm x 25 cm square) randomly installed in each experimental unit. Occurrence of each species was also noted in the same quadrats. Species of *Drepanocladus* genus was not identified at the species level, due to difficulty of identification in the field.

Brown mosses are the dominant vegetation component in Bylot Island polygon fens. Their mean percent cover was about 88 % comparatively to 14 % for vascular plants. *Drepanocladus* sp. is the dominant genus in Bylot wetlands (Table 3.1). Other bryophyte species found in the tundra polygon fens are often present but less abundant (Table 3.1).

3.4.2 Experimental design

In the CW-I experiment, data were taken from a complete randomized block design with four blocks and seven treatments of fertilization (c.f. chapitre 2, section 2.4.2 and table 2.2). Each block was located in a polygon fen and separated at least 500 m from each other. Markers were installed or measured in plexiglas exclosures of 60 cm in diameter and 30 cm high of which at least 20 cm was buried up to the permafrost to prevent leaching or external input of nutrients.

In the WM-I experiment, data were taken from a complete randomized block design with six blocks and 14 treatments of fertilization (c.f. chapitre 2, section 2.4.2 and table 2.2). Each block was situated in a polygon fen and separated at least 500 m from each other. Markers were installed or measured in 2 m x 2 m experimental units (c.f. figure. 2.2) at least 5 m separated from each other to prevent cross contamination between adjacent experimental units.

3.4.3 Estimations of moss stem elongation

Annual elongation was measured in the CW-I experiment with the cranked wire method, as developed by Clymo (1970) for mosses with an upright growing habit. That method was judged suitable for arctic mosses because shoots grow upright in these dense arctic moss carpets (up to 300 000 stems m⁻²; Rochefort, pers. obs.). Smaller cranked wires than those originally used by Clymo (he used cranked wires about 10 cm long under the moss surface; 1970) were fabricated as to be always above the permafrost level during the growth season. Eighteen cranked wires were systematically put in each experimental unit shortly after snowmelt and calibrated. Increases in length were measured at the end of the growing season (mid-August).

Under sharp distinct seasons such as in the High Arctic, several moss species show visible annual growth segment (Clarke *et al.* 1971; Vitt & Pakarinen 1977). On Bylot Island, *Polytrichum strictum* and *Meesia triquetra* have clear seasonal differences in leaf size and spacing (Fig. 3.1). As the growing season cools down, the growth of these mosses slows down resulting in smaller leaves and leaves are closer to each other on the stem, whereas in full summer, leaves are longer and present a large distance between insertion points as the stem elongates also faster (Vitt & Pakarinen 1977). Those two species were used as innate markers. Annual elongation was thus estimated by measuring the distance between top of a stem and the junction between spaced and tight leaves. When it was possible, at least 15 stems of *P. strictum* or *M. triquetra* were collected in each experimental unit on both experimental designs (in CW-I and WM-I experiments) in the middle of August to measure increases in length to the nearest ± 0.1 mm using a binocular in the CW-I experiment and an electronic vernier in the WM-I experiment.

In WM-I experiment, annual elongation was measured by a technique that we named “white marks”. One hundred and sixty stems were marked in each experimental unit using a white insoluble oil-based paint (Painty[®] of ZIG[®], manufactured by Kuretake Co., Ltd.) between June 25th and July 4th, after the drainage of water surplus coming from snowmelt. In 2004, snow cover was inferior to 5 % in the study area in June 17th (Gauthier unpublished data), meaning that marks were done from eight to 17 days after snowmelt. Marks were affixed only during days without rain for facilitating the fixation of the paint. It should be noted, however, that dryness is not a constraint for marking the moss. In fact, the method was originally designed for aquatic mosses (Mati Illomets, University of Tallin, pers. obs.). Forty marks were made in four nests (approximately in a 5 cm x 5 cm square) randomly placed in each experimental unit to easily find the white marks at the end of the season. Marks were all equally made on the stem at 5 mm below the individual moss tip with a fine hair brush, i.e. below the apical bud as to not disturb the growth processes (Fig. 3.1) (see annexe 1 for details). At mid-August, relocated marked mosses were collected and distance from mark to moss tip was measured using an electronic vernier to the nearest ± 0.1 mm. To get the increases in length, the initial 5 mm were subtracted from all measures.

3.4.4 Statistical analyses

For bryophyte stem elongation estimated in the CW-I and WM-I experiments, analyses of variance (ANOVA) for a split-plot, complete randomized block design were performed using the general linear models procedure of SAS (2003). Fertilization treatments were analysed as main plot unit whereas method for estimating stem elongation was the sub-plot unit. Data were tested for homogeneity and normality and were transformed when necessary. We also compared some species or group of species with white marks or innate markers in the WM-I experiment to test if methods gave comparable results from one species to another. *Drepanocladus* sp., *M. triquetra* and *P. strictum* for white mark technique and *M. triquetra* and *P. strictum* for innate marker technique were compared using least square means test because we did not have the same *n* for each category. We included *Drepanocladus* sp. because it was the most abundant group of species present in polygon fens and we wanted to know if results for innate markers were representative of absolute stem elongation values.

Table 3.1 Occurrence (%) and percent cover of species or group of species found in fen polygons. Four quadrats per experimental unit were sampled for percent cover and occurrence were noted inside (n = 336).

Species or group species	Occurrence (%)	Percent cover (mean \pm SE)
<i>Aneura pinguis</i> (L.) Dumort.	4	< 0.5
<i>Aulacomnium palustre</i>	15	1,2 \pm 0,34
<i>Aulacomnium turgidum</i>	32	1,4 \pm 0,24
<i>Brachythecium turgidum</i>	43	0,6 \pm 0,10
<i>Bryum algovicum</i> var. <i>algovicum</i>	51	1,6 \pm 0,32
<i>Bryum cyclophyllum</i>	30	0,5 \pm 0,07
<i>Calliergon giganteum</i>	21	< 0.5
<i>Campylium stellatum</i> var. <i>arcticum</i>	58	1,1 \pm 0,13
<i>Cinclidium arcticum</i>	46	6,6 \pm 0,91
<i>Drepanocladus</i> sp.	100	72,9 \pm 1,24
<i>Meesia triquetra</i>	38	0,9 \pm 0,11
<i>Oncophorus wahlenbergii</i>	2	< 0.5
<i>Polytrichum strictum</i>	49	1,2 \pm 0,12
<i>Meesia triquetra</i> + <i>Polytrichum strictum</i>	88	2,1 \pm 0,23
<i>Sphagnum</i> sp.	11	1,1 \pm 0,29
Total	100	89,6 \pm 0,50

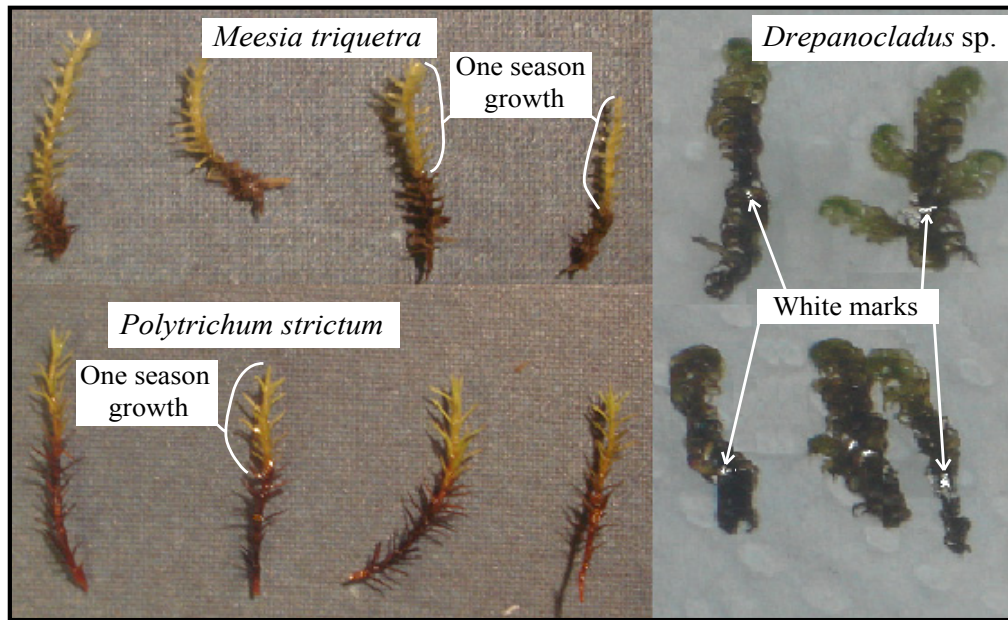


Figure 3.1 Example of annual increment measured on natural innate markers (*Meesia triquetra* and *Polytrichum strictum*) and example of external white marks on stems of *Drepanocladus* sp.

3.5 Results

Data homogeneity and normality were respected for all variables. Only *P. strictum* was used as innate markers in the CW-I experiment (approximately 20 stems per experimental unit). In the WM-I experiment, both *M. triquetra* and *P. strictum* were used as innate markers (approximately 25 stems per experimental unit). About 56 % of white marked stems (approximately 22 stems per experimental units), distributed between 11 species, were found again after the WM-I experimental growing season. Numbers of recovered marked stems by species and their percentage representation were reported in Table 3.2. *Drepanocladus* sp. was the most abundant species with white marks.

In the CW-I experiment, significant difference was found between treatment ($F_{34,14} = 7.96$, $P = < 0.0001$), but no significant difference were found between methods and the interaction of treatments and methods (methods: $F_{34,14} = 4.41$, $P = 0.054$ (Fig 3.2) and treatments*methods: $F_{34,14} = 0.21$, $P = 0.97$). On the other hand, in the WM-I experiment, bryophyte stems elongation estimated with innate markers were significantly greater than those evaluated by white mark method (between 2 and 3 times higher; methods: $F_{137,110} = 128.24$, $P = < 0.0001$; Fig. 3.2). There were also significant difference between treatments ($F_{137,110} = 2.71$, $P = 0.004$), but no significant difference was found in the interaction between methods and treatments ($F_{137,110} = 1.27$, $P = 0.16$). Since interaction between treatments and methods was not significant for both experiments, we present only methods in the figure 3.2. For each method, we have pooled data of all treatments for each species or taxa to simplify the discussion on the comparison of methods only. Least square means test indicated that stem elongation of *P. strictum* with white marks was significantly different from stem increments of *Drepanocladus* sp. and *M. Triquetra* as white marks.

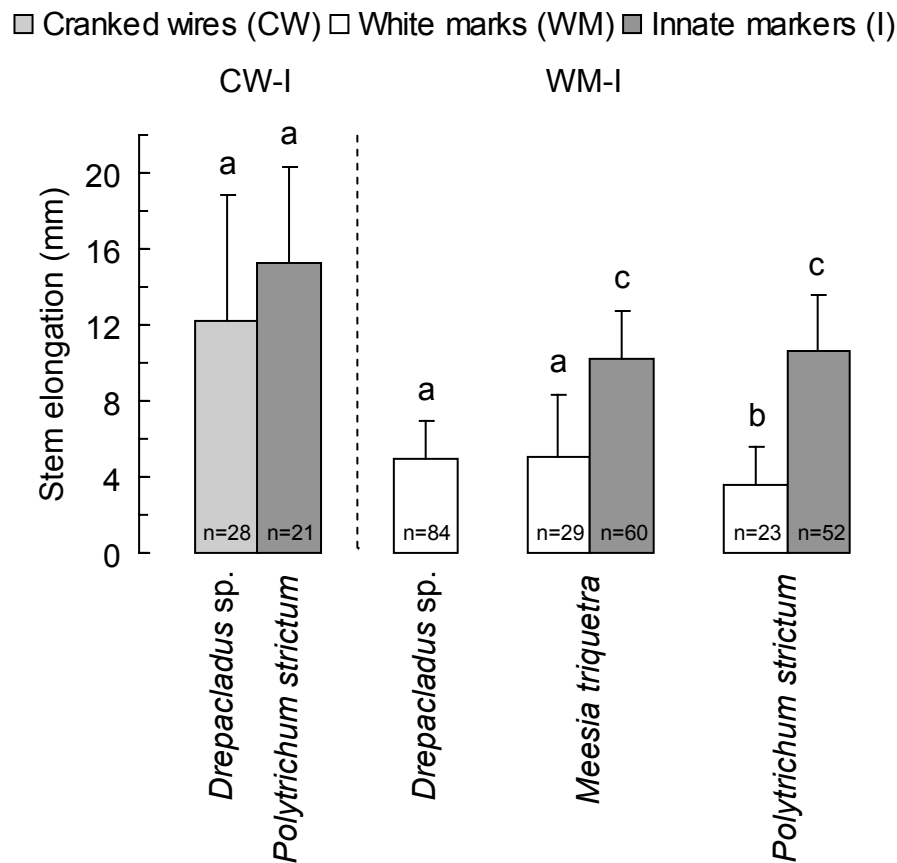


Figure 3.2 Comparisons between stem elongation (mm; means \pm standard deviation) estimated with cranked wires or innate markers in the Cranked Wires – Innate markers (CW-I) experiment and with some species or taxa used as white marks and innate markers in the White Marks – Innate markers (WM-I) experiment. Innate markers are *Meesia triquetra* and *Polytrichum strictum*. The *n* value in each bar corresponds to the number of experimental units. There are approximately 20 innate markers and 18 cranked wires per experimental unit in CW-I experiment. There are approximately 25 innate markers and 22 white marks per experimental unit in WM-I experiment. For the CW-I experiment, no significant difference was found between methods. For the WM-I experiment, different letters indicate significant difference between bars (LS means). Statistical tests were realized per experiment.

Table 3.2 Number of recovered marked stems by species and their percentage representation after 2 months in the field.

Species or group species	Number	%
<i>Aulacomnium palustre</i>	99	1
<i>Aulacomnium turgidum</i>	266	4
<i>Brachythecium turgidum</i>	293	4
<i>Bryum algovicum</i> var. <i>algovicum</i>	399	5
<i>Bryum cyclophyllum</i>	47	1
<i>Calliergon giganteum</i>	204	3
<i>Campylium stellatum</i> var. <i>arcticum</i>	319	4
<i>Cinclidium arcticum</i>	365	5
<i>Drepanocladus</i> sp.	5278	71
<i>Meesia triquetra</i>	71	1
<i>Polytrichum strictum</i>	118	2
Total	7459	100

3.6 Discussion

3.6.1 Alternative methods rejected in this study

Some techniques used to estimate bryophyte stem elongation or primary production are not appropriate for studying arctic polygon fens and they were rapidly eliminated for studies on Bylot Island for the following reasons. Gas exchange technique consists to take an instantaneous measure of photosynthesis and respiration. CO₂ exchange relationships with photosynthetically active radiation (PAR), air temperature, peat temperature and water table are used for modelling net ecosystem production over a season (Bellisario *et al.* 1998; Bubier *et al.* 1999, 2003). It is a useful tool for predicting changes in peatland primary production requiring only few easily measurable environmental variables. However, it is an expensive technique and it needs unwieldy equipment relying heavily on electronics and sources of electricity not necessarily available in remote arctic regions. This method also needs complex calibration and many replicates during the growing season.

As indirect methods, tags or velcro put around the moss stems (Raeymaekers & Glime 1986; Rochefort & Vitt 1988; Li & Glime 1990) or stems cut to a reference level (van der Heijden *et al.* 2000; Pearce *et al.* 2003) are judged not suitable techniques to use in the arctic environment because the stems of the dominant brown mosses are too small and fragile. Furthermore, the disturbance created by isolating individual stem because of the insertion of the marker can impede water conduction and growth potential (Russell 1988).

Another method, autoradiography of tissues with ¹⁴C or ¹⁴CO₂ (Aerts *et al.* 1992, 2001; Wallén 1986; Wallén *et al.* 1988), should be a good alternative to estimate moss stem elongation in polygon fens. It is a relatively inexpensive method (assuming an easy access to radioactivity reading equipment) and is easily adapted to any type of field sites (Russell & Botha 1988). However, it usually involves a fair amount of paper work to obtain autorisations for using radioactive material in natural environments, especially in National Parks, like Bylot Island.

3.6.2 Comparison of three methods using to estimate moss stem elongation in the Arctic

3.6.2.1 Cranked wire method

Since cranked wire method, as developed by Clymo (1970) or with modified wires (Gunnarsson & Rydin 2000; Dorrepaal *et al.* 2004), is the most frequently used in various ecosystems (e.g. Bayley *et al.* 1987; Berendse *et al.* 2001; Camill *et al.* 2001; Chapin *et al.* 2004; Gunnarsson *et al.* 2004; Heijmans *et al.* 2001; Limpens *et al.* 2004; Moore *et al.* 2002; Rochefort *et al.* 1990; Thormann & Bayley 1997; Vitt *et al.* 2003), we first thought that it would be a good choice for Bylot wetlands. In addition, this technique is recommended when substrate is stable, flat and for moss stems growing straight up, like in polygon fens. The modified wires are better anchored into moss carpet than its original version because of the addition of a horizontal piece at the base of each wire. Because of suspected permafrost activities, we used non-modified wires.

In the CW-I experiment, although there was no method difference, it appears that the cranked wire method showed a higher variability than innate marker method (SD = 6.6 mm for cranked wire method and SD = 5.0 mm for innate markers, Fig. 3.2). Because of their intrinsic variability, some indirect methods of moss growth measurement, like cranked wires, are not well adapted to species with small annual increments (Russell 1988). Important sampling variability observed in the CW-I experiment for cranked wire method could be explained by these phenomenons. However, for CW-I experiment, innate markers also showed an important variability, then, other limitations are more important to consider than variability. First, cranked wires were put when experimental units were still flooded by water surplus coming from snowmelt. When water surplus was drained off, the moss carpet got compressed and cranked wires were leaned against permafrost and could have been tied in ice. As a result, cranked wires were maybe not able to follow summer height changes of moss carpet caused by variations of ground water level. Furthermore, this technique was originally planned for *Sphagnum* sp., which has faster growth than arctic brown mosses or for habitats where the *Sphagnum* genus is dominant (Clymo 1970). *Sphagnum* genus is not frequent and not abundant in Bylot Island polygon fens (respectively 11 % and 1.1 %, Table 3.1) and cranked wires are probably not well suited to measure growth of bryophytes

other than *Sphagnum*. As suggested by Lindholm and Vasander (1990), for moss species with a small production, like in arctic polygon fens, measurement markers should be set the year before sampling to avoid interference with moss growth. However, cranked wires are subject to frost-defrost cycle. They cannot be installed the year before sampling to minimize growth interference and then they can cause considerable bias if the study is carried out over several years. For these reasons, we recommend to avoid cranked wire method in arctic wet habitats to measure annual increments if it is possible to use other methods.

3.6.2.2 External white mark method

The use of an insoluble marker to stain bryophyte stems is an interesting and encouraging approach to estimate moss stem elongation. The reason it works for all type of habitat, but mostly for the problematic wet habitat, is that the stain is made with an organic solvent that will evaporate faster than water, so that the target individual stem is not stressed by having to be dry to get their external marker. Russell (1988) had shown external fluorescent markers to be successful in estimating growth for patches of small moss species. On the other hand, another study done in our laboratory testing four different types of dyes (Blancophores BA LIQ, BRS LIQ, CLELIQ, PSC supplied by Miles Canada, a subdivision of Bayer applied at 1%) and one fluorescent brightener (Cellufluor 28 from Sigma applied at 0,1%), all greatly leached out when used for aquatic mosses or in wet habitat (Poulin 1995).

In our study with the oil-based white marker, we have removed bryophytes under water, marked them and replaced them under water. The marker does not leached and marks resist to water immersion. At the end of summer, sampled places at spring did still not appear. Only sticks for nest identification have allowed finding again the marked stems. Moss growth seems to be not affected by remoting moss stem from water for marking. Marks have also resisted when mosses were dried, transported to the laboratory, and then re-wetted to take increment measurements. In addition, drying and re-wetting marked stems before taking growth measures had no effect on stem elongation. Measures taken immediately after harvesting gave exactly the same values than those taken after drying and

re-wetting (data not shown). White mark method is well adapted to polygon fen reality as suggested by a relatively small sampling variability (standard deviation were between ± 2.0 and 3.3 mm, Fig. 3.2). Furthermore, studies using similar procedure to evaluate moss increments (with fluorescent markers or dyes, for example) generally put the marking substrate on moss surface (Russell 1988). Vitt (pers. comm.) affirms that velcro is the best method to use in tundra wetlands because dyes or markers are worrisome and may interfere with photosynthesis. However, Rochefort (personal trial and observation in 1993 and 1994) tried using velcro or tying threads around the small mosses in the wetlands of Bylot Island and both methods isolated the individual marked stem from the carpet causing desiccation of the targeted stem. We do not believe that much interference is caused to the photosynthetic processes in the white mark technique, since we put white marks 5 mm under the apical tip of bryophytes. Furthermore, white mark method was used successfully on many different species, which could further be compared with each other. In addition, marks were made randomly and percentages of recovered marks for each species reflect approximately their real relative abundance observed in experimental units (Tables 3.1 and 3.2).

Nevertheless, some inconveniences of the method must be emphasized. The marking of the stems should be done at the end of the summer preceding sampling period if one needs to capture the early spring growth or make sure to get the closest to absolute annual increments. This means going two years in a row at a remote sampling site. If only relative differences between treatments are needed then this constraint does not hold. To succeed to mark accurately the stems below the apical moss tip, as suggested by our straw window method, it takes time. Time to stain the moss stems, to mark the nest for recovery at the end of measuring period and to measure them again (after one or several seasons as the marks are permanent up to the decomposition of the species in question) should be planned. If one has the possibility to mark stems at the end of growing season that precedes sampling and if needed time to do marks is not a constraint, white mark method should be considered.

3.6.2.3 Innate marker method

Innate markers have been often used to measure moss increments (Camill *et al.* 2001; Clarke *et al.* 1971; Gauthier *et al.* 2004; Potter *et al.* 1995). As several mosses growing in arctic ecosystems show clear seasonality in their growth pattern, this technique should be a good choice if these particular mosses are present in a particular study site. In polygon fens, growth should be relatively homogenous among species because of the growth dynamic of that ecosystem. If a stem grows more rapidly than others, it dries. It only starts again to grow when other stems compensate for the growth difference and when the optimal conditions are back. If a stem grows more slowly than others, it dies by lack of light.

Innate markers, i.e. *M. triquetra* and *P. strictum*, are not very abundant, but they are relatively frequent in Bylot Island polygon fens (in 2004, cover of 2.1 % and occurrence of 88 % when innate marker species are combined). However, we therefore can suppose that innate marker method is representative of real moss stem elongation in those arctic wet habitats. Consequently, *M. triquetra* and *Drepanocladus* sp., the most abundant and frequent taxa (for *Drepanocladus* sp. in 2004, cover of 72.9 % and occurrence of 100 %), showed no significant difference in stem elongation (Fig. 3.2) when both had white marks. Difference between increments estimated with *P. strictum* and others estimated with *Drepanocladus* sp. or *M. triquetra* when both had white marks can be explained by the particular morphology of *P. strictum*. In fact, *P. strictum* count on their rhizoids to absorb water and nutrients. Then, marks could interfere with this process.

Moreover, innate marker method is quick, simple, non destructive because we only have to take few stems and needs only few manipulations. It can be done repeatedly on the same experimental unit during several years (Gauthier *et al.* 2004), by different people, without perturbing the natural environment and without manipulator bias. Comparisons with other studies are also easy to make if the same species are used as innate markers. Since there are generally visible and easily recognizable annual growth segments on these species, we can have stem elongation for the whole growth season and in some case, for precedent growth season(s). Also, this method is well adapted to polygon fen reality as suggested by a relatively small sampling variability (standard deviation were between ± 2.5 and 2.9 mm, Fig. 3.2).

However, adverse environmental conditions may prevent the expression of annual segments (Russell 1988). Innate marker species are not present in all experimental units. In the present case, only 75 % and 87 % of experimental units contain innate markers in the CW-I and WM-I experiments respectively. But, with a sufficient sampling effort, these problems could be avoided. As moss primary production can change quickly according to microtopography, innate markers have to be harvested close to moss samples used to calculate other parameters needed to estimate production. If these conditions are respected, it is probably easier to estimate increments with innate markers in this environment than with other techniques.

3.6.3 Summary

As far as we know, only few studies estimated moss stem elongation in boreal fens, none in tundra polygon fens we did (Table 3.3). Thus, it is important to test some methods in that environment to estimate moss increments with precision.

Cranked wire method is not really adapted to arctic realities especially because polygon fens are subject to surface disturbances. This technique is also not adapted to small brown moss species. So, cranked wire method should be avoided in polygon fens.

It seems that the use of electronic vernier rather than binocular help to reduce sampling variability, as showed by lower variability for innate markers in WM-I experiment (estimated with electronic vernier) than for innate markers in CW-I experiment (measured under binocular). Therefore, in the WM-I experiment, white mark method and innate markers have small and equivalent variability, as showed by low standard deviations. Sampling efforts seem to be adequate, then we suggest to sample 20 stems of innate markers or to recover 20 marked stems per nest with the white marks to have satisfactory estimations of moss stem elongation. Both methods can be appropriate in arctic wetlands and one have to choose the better method according to his study goals.

Since *Drepanocladus* was the most abundant and present genus of bryophytes in polygon fens on Bylot Island (Table 3.1), methods used to estimate moss growth in that habitats must be adapted to this species. From this point of view, technique like white marks seems

to be a good choice, since any particular species can be marked. Indeed, white marks permit marking species proportionally to their abundance. In addition, in contrast to innate markers, white mark method allows the estimation of stem elongation of wet habitat dominant moss species where seasonality is usually not evident. In the WM-I experiment, white marks were done several days after snowmelt. Consequently, measured increments did not reflect the total summer growth whereas innate marker technique did. Significant differences between the techniques in the WM-I experiment may reflect this temporal discrepancy (Fig. 3.2). White mark technique needs to be put in place at the end of the season prior to the year of investigation. However, it is an excellent method to get constant reliable data within an experimental framework and if a lot of time or years are allocated for the experiment because it is possible to see directly the effects of controlled variables on the studied species. It is flexible in its application but more time consuming than the use of innate markers. In fact, a sole visit in the targeted experimental site at the end of a given growing season is sufficient to obtain all measurements needed for innate marker method.

On the other hand, as demonstrated before, innate marker production is representative of real moss stem elongation despite their low relative abundance. Furthermore, advantages of innate marker technique (simple and non destructive method and possibilities of comparisons with others studies) are to be considered. Innate marker method is appropriate to estimate seasonal growth under many climatic conditions without previous weeks or months of preparation and without calibration. It is also a good choice for prepared experimental work when the target species (*Polytrichum* or *Meesia* genus) are relatively frequent in the community and dispersed of a homogeneous way. It is also very appropriate if the experiment includes a lot of sites. However, if innate marker species are not abundant or absent, one have to consider white mark method because it allows the independence of location. Moreover, in places where field costs are high, like in the Arctic, innate markers are definitively the most economical method. Since we have to go on the field only one time, at the end of the growing season, with a restricted team, it will be possible to do substantial economy in term of cost and time.

To conclude, innate markers like *P. strictum* or *M. triquetra* are the best method to use if study goal is to estimate global moss increments in arctic polygon fens. White mark method

is more appropriated for studies aiming to evaluate growth of a particular moss species or to compare increments of different species. With some improvements, white marks stems technique using the same kind of insoluble paint that we used could become a great choice for any moss species in any conditions whereas innate markers are easier to manipulate and should be preferred in study where appropriate species are present.

Table 3.3 Methods used in fen productivity studies.

Method	Study location	Type of bryophytes	Source
Cranked wires	Québec	<i>Sphagnum</i>	Bartsch & Moore 1985
Cranked wires	Minnesota	<i>Sphagnum</i>	Chapin <i>et al.</i> 2004
Cranked wires	Alberta	<i>Sphagnum</i> and <i>Tomenthypnum nitens</i>	Li & Vitt 1997
Cranked wires	Ontario	<i>Sphagnum</i>	Rochefort <i>et al.</i> 1990
Cranked wires	Alberta	<i>Sphagnum</i>	Szumigalski & Bayley 1996
Cranked wires	Alberta	<i>Sphagnum</i>	Thormann & Bayley 1997
Direct harvest	Switzerland	All present species	Bergamini <i>et al.</i> 2001
Gas exchange	Manitoba	All present species	Bubier <i>et al.</i> 1999
Velcro	Alberta	<i>S. scorpioides</i> and <i>T. nitens</i>	Rochefort & Vitt 1988
Velcro	Alberta & Netherlands	<i>S. scorpioides</i>	Vitt <i>et al.</i> 1993

Conclusion générale

4.1 Quel est le rôle des mousses dans les interactions trophiques présentes sur les polygones de tourbe ?

Cette étude a permis de confirmer la nature des limites nutritionnelles présentes dans les polygones de tourbe. Comme ce fut le cas dans l'étude de Pineau (1999), la croissance des plantes graminoides est limitée par l'azote tandis que celle des mousses ne présente pas de limite nutritionnelle particulière (pour le N ou le P). La croissance des mousses est davantage favorisée par une addition combinée de N et de P comparativement à l'un ou l'autre des nutriments ajouté seul. Par contre, ce n'est pas le cas pour les plantes graminoides. L'ajout de glycine ne favorise pas davantage la croissance des plantes graminoides et des mousses qu'un ajout équivalent de N inorganique ($1 \text{ g} / \text{m}^2$), ce qui peut être dû à la durée de l'expérience avec la glycine (seulement testé sur un an).

Puisque les plantes graminoides sont limitées par le N, l'effet fertilisant des oies sera davantage un effet azoté. En effet, l'ajout de fèces a bel et bien le même effet qu'un ajout équivalent de N ($1 \text{ g} / \text{m}^2$) sur la croissance des plantes graminoides ou des mousses. De plus, il est généralement accepté qu'une interaction entre les plantes graminoides broutées et les mousses existent dans le cycle des éléments nutritifs (Shaver et Chapin 1995). Qu'en est-il pour les polygones de tourbe de l'île Bylot ?

Les mousses bénéficient de l'apport soudain en nutriments provenant des fèces d'oies et séquestrent les nutriments au détriment de celle des plantes graminoides. Cette étude a ainsi permis de valider l'hypothèse du tapis de bryophytes émise par Gauthier *et al.* (1996), Pineau (1999) et Kotanen (2002). Les différences rencontrées entre les études de fertilisation en Arctique sont très reliées à la présence ou non d'un tapis de bryophytes. Les mousses deviennent saturées en nutriments suite à l'addition des doses les plus élevées (égales ou supérieures à $5 \text{ g} \text{ de N} / \text{m}^2$). On observe une augmentation du contenu en N dans les bryophytes et une amélioration de la croissance des plantes graminoides au fur et à mesure que les additions de N augmentent. Par contre, les taux de décomposition et le recyclage des éléments nutritifs ne sont pas favorisés par l'augmentation des doses de N. Il semble que l'apport additionnel de N soit presque totalement absorbé avant d'atteindre la couche microbienne active puisque le contenu en N augmente très peu dans la matière

organique dans les sacs en décomposition. La quantité qui atteint la couche microbienne n'est cependant pas suffisante pour augmenter la décomposition.

Le rôle des bryophytes est donc vraiment important dans les polygones de tourbe de l'île Bylot. Les mousses modifient l'interaction classique entre les plantes broutées et l'herbivore en séquestrant les nutriments ajoutés par les fèces d'oies et en ayant ainsi un impact négatif indirect sur les plantes graminoides. En fait, les oies ont un effet négatif sur les plantes graminoides en les broutant (Gauthier *et al.* 1995; 1996), et de plus, leurs fèces n'aident pas la croissance après le broutement comme c'est généralement le cas dans d'autres environnements (e.g. Bazely et Jefferies 1985). Éventuellement, les nutriments seraient lentement relâchés via la décomposition du tapis de mousse et graduellement transférés aux racines des plantes graminoides broutées, comme ce fut suggéré pour d'autres communautés dominées par les mousses (Marion *et al.* 1982; Li et Vitt, 1997). D'autres expériences sont donc nécessaires pour explorer les effets à long terme des fèces d'oies sur la production primaire des mousses ou des plantes graminoides, les taux de décomposition et le recyclage des nutriments dans les polygones de tourbe.

4.2 Quelle est la meilleure méthode pour estimer la production des bryophytes ?

À chaque fois qu'un chercheur décide d'estimer la production primaire des bryophytes, il doit choisir la méthode d'estimation la plus appropriée pour les espèces étudiées et le milieu dans lequel elles vivent. Cette étude a démontré que, pour les polygones de tourbe des régions arctiques, la méthode des marqueurs naturels est la plus appropriée surtout si le but de l'étude est d'estimer l'élongation global des mousses. Par contre, les marqueurs naturels doivent être distribués de façon homogène dans le milieu. Cette méthode est simple, facilement répétable, non destructrice et ne nécessite pas beaucoup de préparation. Elle permet également de faire des économies de temps et d'argent dans un milieu où les déplacements sont difficiles et coûteux. La méthode des marqueurs permanents blancs, quant à elle, nécessite une précision importante, beaucoup de temps et est destructrice. Elle doit aussi être mise en place l'année qui précède l'année d'échantillonnage pour avoir une estimation de la saison de croissance complète. Par contre, dans une perspective d'étude à

long terme, cette méthode permettrait d'obtenir des données très fiables et diversifiées. De plus, elle permet d'estimer la production pour une espèce particulière de bryophyte et ainsi, favorise les comparaisons entre les espèces. Également, le type de marqueurs utilisés dans cette étude résiste à plusieurs conditions. Par exemple, il peut être mis sur des tiges qui seront immergées et les tiges peuvent être séchées et remouillées sans que les marqueurs ne disparaissent ou ne se délavent. Finalement, la méthode des tiges coudées n'est pas adaptée aux polygones de tourbe, principalement parce que le soulèvement gélival et les inondations y sont des événements fréquents.

4.3 Ajout de nutriments et changements climatiques

Dans une perspective à long terme, il est important de se demander quel le facteur peut potentiellement influencer le plus l'écosystème étudié. Dans le cas des milieux humides de l'île Bylot, est-ce la population d'oies ou la présence des tapis de mousse ? Les mousses ont un effet indirect sur les plantes broutées. Par contre, les plantes broutées profitent des nutriments relâchés par la décomposition de la partie plus âgée du tapis de mousse. Les oies sont présentes sur l'île Bylot depuis plusieurs décennies et elles ont modifié le milieu. En effet, les oies contribuent à maintenir un équilibre dans les polygones de tourbe dans lequel la production de plantes graminoides est plus faible comparativement à la situation où les oies seraient absentes du système (Gauthier *et al.* 2004). Un autre facteur doit cependant être pris en considération pour être en mesure de prévoir ce qui se passera dans les polygones de tourbe au cours des prochains siècles: les changements climatiques. Le réchauffement climatique peut avoir un impact direct sur toutes les composantes présentes dans les polygones de tourbe et y modifier les interactions trophiques. Un des effets probables du réchauffement des températures est que la décomposition serait favorisée et que davantage de nutriments seraient disponibles pour la croissance de tous les types de plantes (Weintraub et Schimel 2005). Cette étude, en ajoutant des nutriments dans l'écosystème, simule en quelque sorte un effet potentiel des changements climatiques. Il serait donc intéressant, voir même essentiel, de poursuivre ces recherches dans le but d'améliorer notre compréhension du réchauffement global sur les écosystèmes arctiques.

Il est bien connu que les modèles de circulation globale (*General Circulation Models*, GCM) prédisent une augmentation des températures en Arctique. Dans l'Arctique de l'est canadien, où l'île Bylot est située, la moyenne pour quatre GCMs prédit une hausse de 3.5 à 8.5°C, selon la saison, si les concentrations actuelles de gaz à effets de serre doublent (Maxwell 1992). Même si les hausses de température les plus importantes surviendraient typiquement durant l'hiver, la saison de croissance serait aussi plus chaude. Les sols de plusieurs écosystèmes arctiques, généralement humides et présentant de faibles températures, contiennent de grandes quantités de carbone organique potentiellement décomposable qui pourraient être perdues sous des conditions climatiques plus chaudes ou plus sèches (Nadelhoffer 1992). Le réchauffement climatique pourrait ainsi accélérer la décomposition de la matière organique et la minéralisation des nutriments dans les sols arctiques et, de ce fait, augmenter la disponibilité des nutriments (Weintraub et Schimel 2005). De plus, l'élévation plus marquée des températures durant l'hiver pourrait causer une augmentation de l'épaisseur de la couche de neige et ainsi créer une hausse de la minéralisation du N puisque les températures du sol demeureraient plus élevées à cause de l'effet isolant de la neige (Schimel *et al.* 2004). Le N relâché par la matière organique pourrait aussi favoriser la croissance des plantes, donc l'accumulation du carbone dans le milieu. Cependant, puisque la couche microbienne active aurait accès en premier à ce relâchement supplémentaire de nutriments, les changements dans la disponibilité des nutriments pour les plantes dépendraient de l'étendue de leur immobilisation par les micro-organismes (Jonasson *et al.* 1993). Si les micro-organismes utilisent une quantité supérieure de nutriments provenant du surplus amené par l'élévation des températures que la quantité utilisée par les plantes, la décomposition sera davantage favorisée que la production. Ce relâchement projeté des nutriments présents dans le sol associé avec une hausse des températures marquée sous les latitudes élevées pourrait donc amplifier le relâchement du carbone du sol, ce qui causerait une perte nette de carbone dans les toundras humides et un feed-back positif sur le réchauffement climatique (Mack *et al.* 2004).

L'ajout anthropique de nutriments dans un milieu augmente la réserve totale de nutriments et la quantité qui est disponible. La hausse des taux de décomposition et du recyclage des éléments nutritifs, comme prédit par l'hypothèse des changements globaux (Gorham 1991; Weintraub et Schimel 2005), maintient quant à elle la même réserve de nutriments et

augmente simplement la proportion qui est disponible. Cependant, les expériences ajoutant artificiellement des nutriments dans un environnement particulier peuvent donner un aperçu des effets possibles du réchauffement climatique.

Sur l'île Bylot, après deux années de fertilisation, la production aérienne des plantes graminoides est favorisée uniquement à des additions égales ou supérieures à 5 g de N / m² et les taux de décomposition ne sont pas favorisés. À l'opposé, après deux ans, les taux de décomposition sont favorisés par l'application d'une même dose de N (5 g / m²) dans une lande d'arbustes nains au nord de la Suède (Robinson *et al.* 1995). Il est donc important de considérer l'environnement dans lequel l'étude a été faite avant de faire des conclusions générales sur les effets de la hausse de la disponibilité des nutriments causée par les changements climatiques. Dans une étude effectuée dans une lande subalpine au nord de la Suède, la biomasse des plantes vasculaires est fortement favorisée mais celle des bryophytes est diminuée après 4 ans d'un traitement combiné de fertilisants (10 g de N / m²; 2,6 g de P / m²; 9 g de K / m² et 0,8 g de Mg / m²) et de hausse des températures (~ 4°C) (Jonasson *et al.* 1999). Dans une tourbière minérotrophe au Minnesota après 6 ans de fertilisation, les communautés microbiennes responsables du cycle du carbone dans le sol sont tolérantes à une grande variation de concentrations de nutriments (2 ou 6 g de N / m² avec 0,67 ou 2 g de P / m²) et seraient relativement insensibles aux stress anthropiques futurs (Keller *et al.* 2005). Dans ce cas, les émissions de carbone ne sont donc pas favorisées par les additions de nutriments. Cependant, dans une toundra humide en Alaska, l'augmentation de la disponibilité des nutriments (fertilisation avec 10 g de N / m² avec 5 g de P / m² pendant 20 ans) a causé une perte nette de 2000 g / m² de carbone dans une toundra humide de l'Alaska et ce, même si la production aérienne des plantes a doublé (Mack *et al.* 2004). Dans ce cas, l'effet est donc plus marqué sur la décomposition que sur la productivité des plantes. Suite à ces quelques observations, il semble que la hausse de la disponibilité des nutriments ait un effet de plus en plus important avec le temps.

Si le même processus survient avec le temps dans les polygones de tourbe de l'île Bylot, où un épais tapis de mousse est présent, la décomposition sera favorisée et cela pourrait produire une cascade d'effets. La production des plantes graminoides pourrait être augmentée puisqu'il y aurait davantage de nutriments disponibles, ce qui risquerait de

diminuer celle des bryophytes à cause de l'augmentation de l'ombre créée par les plantes graminoides. En effet, les mousses sont favorisées sous une combinaison de radiation et d'humidité optimale pour leur croissance (Bergamini *et al.* 2001). Cette combinaison optimale serait modifiée par l'augmentation des plantes graminoides. Le tapis de mousse deviendrait plus mince et l'accumulation de la tourbe diminuerait. Les interactions trophiques entre les oies, les plantes graminoides et les mousses pourraient aussi être modifiées. Les changements climatiques pourraient modifier complètement la dynamique des polygones de tourbe sur l'île Bylot. Cependant, d'autres expériences sont nécessaires pour bien comprendre les effets possibles du réchauffement global dans ces écosystèmes fragiles, à court et à long termes.

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ANNEXE 1 – Schématisation du marquage des mousses

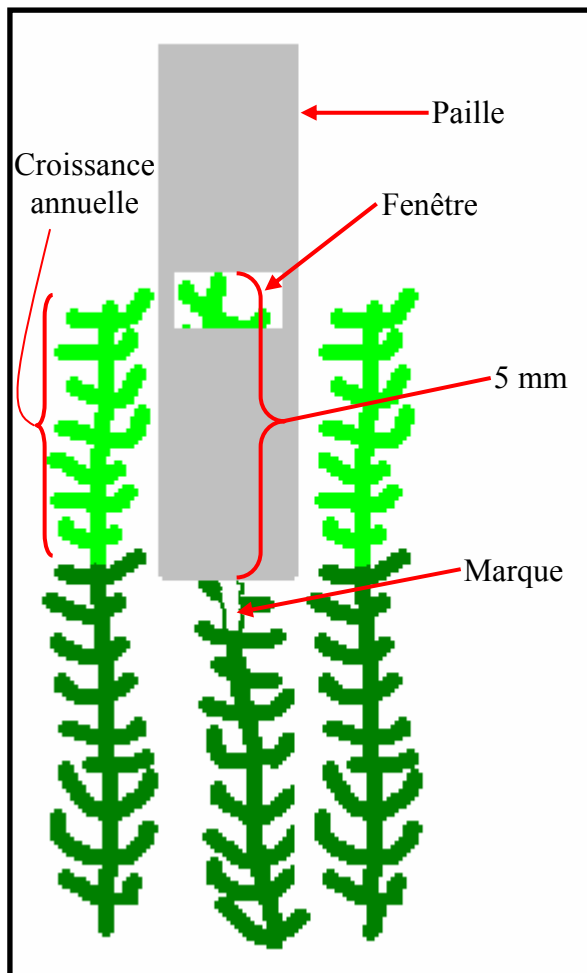


Figure A1 Schématisation de la technique de marquage des tiges de bryophytes avec le marqueur blanc insoluble.

Voici un résumé de la technique utilisée dans l'expérience WM-I du chapitre deux pour marquer les tiges de bryophytes avec le marqueur blanc insoluble :

- 1) Découper une fenêtre dans une paille de plastique au niveau désiré. Dans mon cas, le haut de la fenêtre est situé à 5 mm du bas de la paille.
- 2) Sur le terrain, prendre un échantillon de tourbe (environ 5 cm x 5 cm) et noter l'endroit où il a été pris. Laisser s'égoutter.
- 3) Insérer une tige de bryophytes dans la paille en s'assurant que le sommet de la tige est situé au même niveau que le haut de la fenêtre.
- 4) Faire la marque avec le marqueur insoluble directement sous la paille. La marque peut être assez grosse, en autant qu'elle ne dépasse pas l'extrémité inférieure de la paille.
- 5) Remettre l'échantillon de tourbe avec les individus marqués à sa place dans l'unité expérimentale.
- 6) À la fin de la période pour laquelle on désire avoir une mesure de croissance, reprendre les échantillons de tourbes et récupérer les individus marqués. Les mettre

dans des petites pochettes de papier journal et les faire sécher. Lors des prises de mesure, bien réhumidifier les tiges de bryophytes.

Notes : Le fait de prendre un échantillon de tourbe et de le remettre à sa place après avoir marqué les tiges n'a pas influencer la croissance. À la fin de l'été, les endroits échantillonnés au printemps ne paraissaient plus, seul les bâtonnets de bois insérés dans la tourbe aux endroits échantillonnés nous ont permis de retrouver les tiges marquées. Le fait de sécher et de réhumidifier les tiges avant de mesurer la croissance n'a pas d'effet sur la prise de mesure. J'ai fait des tests pour le savoir en mesurant des tiges immédiatement après la récolte et après un séchage et une réhumidification et il n'y avait pas de différences sur les mesures.

ANNEXE 2 – Schématisation de la prise de biomasse pour les plantes vasculaires

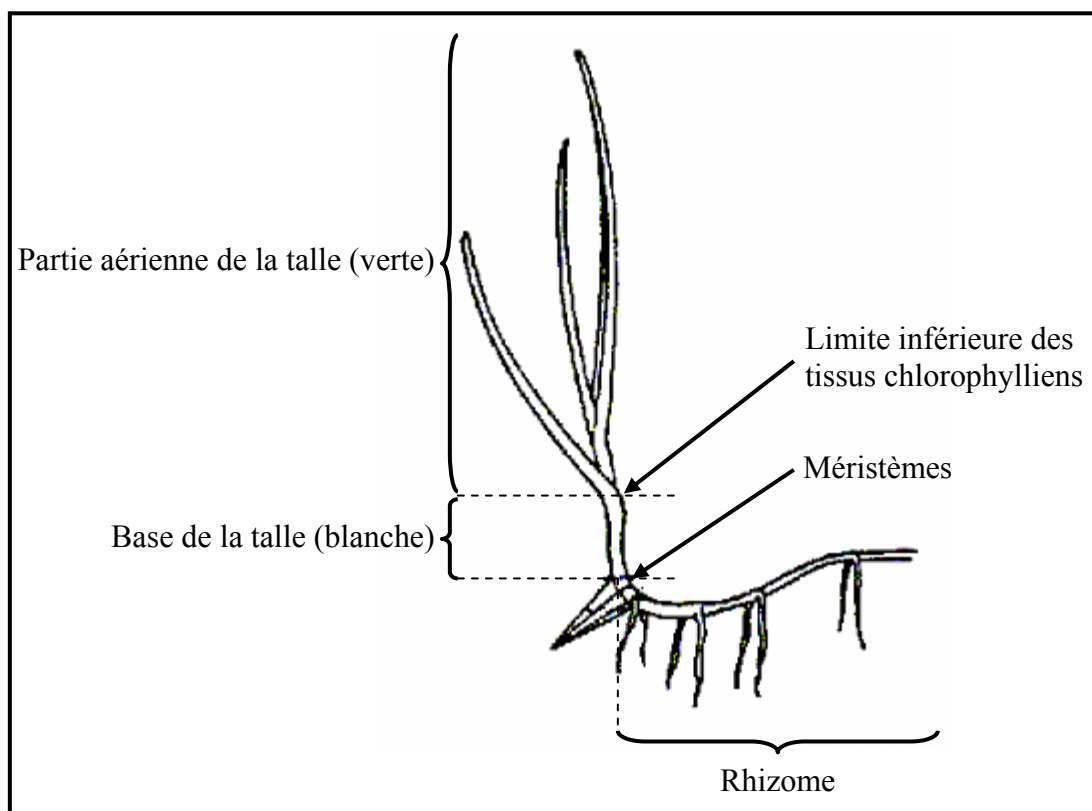


Figure A2 Schéma d'une plante graminéoïde trouvée sur l'île Bylot.

Note : Pour les mesures de biomasse, seulement la partie aérienne verte de la talle et sa base (partie blanche) ont été conservées.