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EFFET DE LA PROLIFÉRATION DU HÊTRE SUR LA TRANSPIRATION DE L'ÉRABLE À SUCRE

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

DBH   Diameter at Breast Height

GLMM   Generalized Linear Mixed Model

LAI   Leaf Area Index

RCP   Representative Concentration Pathway

VPD   Vapor Pressure Deficit

RÉSUMÉ

La formation de végétation récalcitrante de sous-bois, un phénomène observé dans divers types de forêts dans le monde, peut limiter la régénération des arbres et, à long terme, modifier la composition, la succession et le bilan hydrique des forêts. Dans les forêts tempérées du sud du Québec (Canada), la prolifération du hêtre à grandes feuilles (*Fagus grandifolia*) dans les peuplements dominés par l'érable à sucre (*Acer saccharum*) est apparentée au phénomène de végétation récalcitrante. De plus, avec une augmentation prévue de la sévérité et de la durée des sécheresses, une meilleure compréhension des effets de la prolifération du hêtre sur les flux hydriques est cruciale pour comprendre la trajectoire des forêts. L'objectif de cette étude était de comprendre comment la végétation récalcitrante, en l'occurrence la prolifération du hêtre dans les érablières, influence l'utilisation de l'eau par les arbres. Nous avons comparé la transpiration i) des arbres de la strate supérieure (c'est-à-dire les érables à sucre) et ii) des gaules de la strate inférieure (c'est-à-dire le hêtre) dans des sites avec et sans sous-étage dominé par le hêtre. À chacun des six sites, nous avons mesuré la densité de flux de sève (F_d) de deux érables à sucre (diamètre à hauteur de poitrine > 9 cm) et d'une gaule de hêtre (1 cm < diamètre à hauteur de poitrine < 9 cm) à l'aide de capteurs de dissipation thermique pendant la saison de croissance. À l'échelle de l'arbre, le F_d des érables à sucre était significativement plus grand dans les sites dominés par le hêtre en comparaison aux sites témoins indiquant ainsi une plus grande consommation de l'eau par l'érable à sucre lorsque la végétation de sous-étage est dominée par le hêtre. A l'échelle du peuplement, la transpiration totale a varié entre 140 et 296 mm pour la période d'étude, sans différence significative entre les sites dominés par le hêtre et les sites témoins. Nous avançons deux hypothèses pour expliquer nos résultats à l'échelle de l'arbre : i) un moindre développement de la végétation au sol limiterait la transpiration par cette strate de végétation permettant ainsi une disponibilité accrue des ressources en eau pour alimenter la transpiration des arbres ou ii) le taux de transpiration accru des arbres serait un mécanisme pour satisfaire les besoins en éléments nutritifs dans les peuplements dominés par le hêtre, souvent associés à une faible fertilité du sol. Des recherches supplémentaires sont nécessaires pour mieux comprendre les mécanismes régissant l'utilisation de l'eau par les arbres face à la prolifération du hêtre.

Mots clés : *Fagus grandifolia*, *Acer saccharum*, utilisation de l'eau par les arbres, végétation récalcitrante de sous-bois, dominance du hêtre, densité de flux de sève, transpiration

CHAPITRE 1
INTRODUCTION GENERALE

1.1   Problématique

On observe une progression importante du hêtre à grandes feuilles (*Fagus grandifolia*, ci-après hêtre) et un déclin de l'érable à sucre (*Acer saccharum*) dans les forêts décidues du sud du Québec, y compris en Outaouais (Direction de la recherche forestière, 2017). Bien que ces deux espèces aient coexisté depuis des siècles (Poulson et Platt, 1996), la prolifération du hêtre entraîne un changement de composition des peuplements forestiers (Duchesne *et al.*, 2005). La densité des gaules de hêtre a doublé sur une période de 10 ans dans la plupart des forêts décidues du Québec et celle de l'érable à sucre a diminué de 20 % au cours de la même période (Duchesne *et al.*, 2005). Avec la prévalence de la maladie corticale du hêtre qui fait que peu de hêtres matures survivent (Ehrlich, 1934 ; Kasson et Livingston, 2012 ; Roy et Nolet, 2018), la prolifération du hêtre peut changer la composition forestière vers un peuplement monospécifique composé de gaules et de perches de hêtre. Cette modification a un impact subséquent sur la fourniture de services écosystémiques par ces forêts (approvisionnement en bois, habitat, production de sirop d'érable, stockage de carbone). Étant donné la faible valeur marchande du hêtre, la mortalité des arbres matures due à la maladie corticale du hêtre est également peu favorable pour l'industrie forestière.

La prolifération du hêtre présente des caractéristiques similaires au développement de la végétation récalcitrante de sous-bois, un phénomène qui s'observe à l'échelle mondiale où une couche dense et persistante de végétation herbacée ou arbustive se développe et empêche la régénération de certaines espèces d'arbres appartenant à la canopée (George et Bazzaz, 1999a ; Roy et Nolet, 2015 ; Royo et Carson, 2006). Il en résulte ainsi un changement de la composition des peuplements. En effet, la progression de végétations récalcitrantes peut inhiber la régénération d'autres espèces via divers mécanismes d'interférence tels que la compétition pour les ressources (lumière, eau, éléments nutritifs), l'allélopathie (inhibition chimique), l'accumulation de la litière, la prédation des semis par les petits mammifères et les dommages mécaniques (Royo et Carson, 2006). Si diverses études ont permis de mieux comprendre le rôle de la compétition pour la lumière comme mécanisme d'interférence (Beckage *et al.*, 2000 ; Messier *et al.*, 1998 ; Nilsen *et al.*, 2001b), peu d'études se sont intéressées au mécanisme de compétition pour l'eau. L'effet des végétations récalcitrantes sur la compétition pour les

ressources en eau reste peu documenté bien que la formation de cette couche dense de sous-bois pourrait venir modifier le bilan hydrique des forêts, et par conséquent la disponibilité des ressources en eau pour les arbres.

Face à l'augmentation projetée de la fréquence et de la sévérité des sécheresses avec les changements climatiques (Trenberth *et al.*, 2014), il s'avère particulièrement important de comprendre l'effet de la prolifération du hêtre sur l'utilisation de l'eau par les arbres afin de bien évaluer la trajectoire à long terme de ces peuplements forestiers. Au Québec, les projections climatiques futures indiquent une augmentation de la température moyenne de 4 à 7 °C pour la période 2071-2100 avec un scénario de fortes émissions RCP 8,5, par rapport à la période de référence 1970-2000 (Ouranos, 2015). L'augmentation des températures se traduit par une demande évaporative accrue pendant la saison de croissance, favorisant l'évapotranspiration et un possible épuisement des ressources en eau du sol. De plus, un allongement des jours consécutifs sans précipitations est projeté durant la saison estivale (Donat *et al.*, 2013 ; Ouranos, 2015) venant ainsi limiter l'apport en eau pendant la saison de croissance. La diminution des ressources en eau disponible du sol peut mener à un stress hydrique et, par conséquent, une importante compétition des arbres pour les ressources en eau (Gleason *et al.*, 2017), d'où l'importance de bien comprendre l'effet de la prolifération du hêtre sur l'utilisation des ressources hydriques.

1.2   Prolifération du hêtre dans les érablières

Un changement de la composition des forêts tempérées décidues a été constaté au cours des deux derniers siècles (Brisson et Bouchard, 2003). De nombreuses études (Bose *et al.*, 2017 ; Cale *et al.*, 2013 ; Houston, 2001) ont fait état d'une dense couche de hêtre avec plus de 1500 gaules à l'hectare dans des peuplements dominés par l'érable à sucre (Duchesne *et al.*, 2005 ; Nolet *et al.*, 2008). Cette dense couche de hêtre vient limiter la disponibilité de la lumière sous la canopée, ce qui affecte négativement la régénération de l'érable à sucre (Beaudet *et al.*, 1999 ; Collin *et al.*, 2017 ; Hane, 2003). Par ailleurs, la prévalence de la maladie corticale du hêtre dans le Québec méridional fait en sorte que peu de hêtres matures survivent (Roy et Nolet, 2015) ce qui a un impact considérable sur la dynamique des peuplements forestiers.

La progression du hêtre dans les érablières se manifeste par le développement d'une strate dense et persistante (jusqu'à 5 m^2/ha de gaules et de perches de hêtre) (Roy et Nolet, 2015). Dans les forêts nord-américaines, ce développement progressif du hêtre peut être favorisé par de

nombreux facteurs tels que : l'ouverture de la canopée, les caractéristiques du sol, l'herbivorie et les changements globaux. Premièrement, le hêtre est une espèce plus tolérante à l'ombre, avec une plus grande capacité de survie et de croissance sous des canopées fermées par rapport à l'érable à sucre (Beaudet et Messier, 1998 ; Canham, 1988 ; Messier et Nikinmaa, 2000). De plus, les semis de hêtre ont un taux de croissance similaire, voire plus élevé que l'érable à sucre, sous des régimes de luminosité élevée suite à l'ouverture de la canopée (Beaudet *et al.*, 2007 ; Takahashi et Lechowicz, 2008) notamment par des coupes partielles (Bannon *et al.*, 2015 ; Nolet *et al.*, 2008). Le développement du hêtre suite à l'ouverture de la canopée crée des conditions désavantageuses pour l'établissement de l'érable à sucre dû à la réduction de la lumière disponible (Collin *et al.*, 2017). Deuxièmement, le hêtre a une capacité d'adaptation accrue sur les sols peu fertiles ou acides (Halman *et al.*, 2015 ; Kobe *et al.*, 2002). En effet, le pH du sol et la disponibilité des éléments nutritifs, notamment le calcium et l'aluminium, présentent des facteurs déterminants de la répartition du hêtre et de l'érable à sucre (Arii et Lechowicz, 2002 ; Duchesne et Ouimet, 2009). Une faible teneur en Ca du sol ou une concentration élevée en Al n'ont pas d'effets significatifs sur la croissance radiale des gaules de hêtre (Halman *et al.*, 2015). Cependant, une faible teneur en Ca du sol réduirait le taux de croissance de l'érable à sucre (Duchesne *et al.*, 2002 ; Long *et al.*, 2009). Le hêtre serait ainsi avantagé sur les sols forestiers affectés par les dépôts atmosphériques acides, où les nutriments, dont le Ca et Mg, sont éliminés (Duchesne et Ouimet, 2009 ; Federer *et al.*, 1989). Par ailleurs, la lente décomposition de la litière de hêtre, due à sa composition élevée en lignine (Melillo *et al.*, 1982) entraîne un pH faible pouvant exacerber l'appauvrissement en éléments nutritifs du sol (Côté et Fyles, 1994). Troisièmement, le hêtre peut être favorisé dans les peuplements feuillus étant donné la faible appétence du cerf de Virginie (*Odocoileus virginianus*) pour cette espèce et sa préférence pour d'autres feuillus, comme l'érable à sucre (Long *et al.*, 2007 ; Nyland *et al.*, 2006). Cela peut jouer un rôle considérable dans la régénération du hêtre étant donné l'importance de l'herbivorie dans certaines régions (Sage *et al.*, 2003 ; Tremblay *et al.*, 2007). Quatrièmement, les changements globaux actuels sont également des facteurs non négligeables de la progression du hêtre et du déclin de l'érable à sucre. L'érable à sucre est plus adapté à un environnement frais et humide, tandis que le hêtre a un meilleur développement dans un environnement chaud et sec (Direction de la recherche forestière, 2017). Le réchauffement de la température durant la saison de croissance et les conséquences sur le bilan hydrique des peuplements constituent des facteurs déterminants de l'expansion du hêtre à grande feuille et du déclin de l'érable à sucre (Bose *et al.*, 2017 ; Direction de la recherche forestière, 2017 ; Payette *et al.*, 1996). En termes de changements globaux, la prévalence de la

maladie corticale du hêtre favorise également l'expansion de cette espèce. Cette maladie, introduite en Nouvelle-Écosse en 1929 (Ehrlich, 1934), résulte de l'interaction entre la cochenille du hêtre (*Cryptococcus fagisuga* Lindinger.) et deux champignons pathogènes (*Neonectria ditissitima* et *Neonectria faginata*) (Cale *et al.*, 2017). La maladie corticale du hêtre est présente et a commencé à infecter la région de l'Outaouais au moins depuis 2013 (Ministère des Forêts, de la Faune et des Parcs, 2020 ; Roy et Nolet, 2015). Cette maladie fait en sorte que peu de hêtres matures survivent (Cale *et al.*, 2017 ; Roy et Nolet, 2018); il en résulte ainsi une couche dense formée de gaules de hêtre. En effet, plusieurs études ont démontré une augmentation de la densité des gaules de hêtre, allant jusqu'à 350 %, après une infestation par la maladie corticale du hêtre (Cale *et al.*, 2013 ; Garnas *et al.*, 2011 ; Houston, 2001).

1.3   Impacts des changements climatiques sur le bilan hydrique forestier

Le climat du Québec évolue avec le climat mondial (Cohen *et al.*, 2019). La température et les précipitations sont les principales variables surveillées (Zhang *et al.*, 2019) pour étudier l'ampleur des changements climatiques. La température a augmenté de plus de 0,7 °C sur le plan mondial de 1986 à 2016 (USGCRP, 2017), et de 1,1 °C pour le Québec de 1948 à 2016, soit presque le double de l'augmentation observée à l'échelle mondiale (Cohen *et al.*, 2019). L'évolution des précipitations estivales montre également une augmentation d'environ de 6,6 % de 1948 à 2012 pour le Québec (Zhang *et al.*, 2019).

Pour le sud du Québec, les projections futures du climat montrent une augmentation de la température moyenne de 3,9 à 7,2 °C en période estivale (mois de juin à août) sous un scénario d'émissions élevées RCP 8,5 (Horizon 80) (Ouranos, 2015). Les périodes de vague de chaleur vont également augmenter en durée et en fréquence, ainsi que les nuits chaudes avec une température minimale supérieure à 20 °C (Bonsal *et al.*, 2019 ; Ouranos, 2015). Concernant les précipitations annuelles, une augmentation de l'ordre de 5 % à 15 % est prévue dans le sud du Québec selon les trajectoires RCP 4,5 et 8,5 (Ouranos, 2015). Toutefois, une diminution des précipitations estivales est prévue vers la fin du siècle selon la trajectoire RCP 8,5 (Cohen *et al.*, 2019). De plus, un allongement des périodes sans précipitation est prévue pour la saison estivale pour l'horizon 2081-2100 (Ouranos, 2015). Un allongement moyen de la saison de croissance d'environ 20 jours est également attendu pour 2041-2070 (Audet *et al.*, 2012 ; Logan *et al.*, 2011), ce qui pourrait mener à un épuisement des ressources en eau du sol.

Dans l'ensemble, l'augmentation des températures et la modification du régime de précipitation aura des conséquences sur le bilan hydrique qui peuvent se traduire par la diminution de l'humidité du sol : les projections sur l'humidité du sol prévoient une diminution de 20 à 40 % pour la période 2070-2099 en comparaison à la période contemporaine (Houle *et al.*, 2012). L'assèchement projeté des sols touchera principalement la couche de surface, soit les dix premiers centimètres, avec un impact moindre dans les couches de profondeur (Berg *et al.*, 2017 ; Seneviratne *et al.*, 2012). L'humidité du sol réduite peut mener à la création d'un stress hydrique pour la végétation. La forte compétition entre les arbres pour les ressources en eau constitue un des principaux facteurs de mortalité des arbres à l'échelle globale (Allen *et al.*, 2010 ; Gleason *et al.*, 2017) . Les forêts nord-américaines n'y font pas exception : le taux annuel de mortalité liée aux changements dans le bilan hydrique est passé de 1,1 % à 2 % de 1951 à 2014 (Hember *et al.*, 2017) sachant que la sécheresse affecte 10 à 15 % des peuplements dans les forêts tempérées décidues (Allen *et al.*, 2010). La limitation des ressources en eau a également entrainé une baisse de productivité des forêts et accru la mortalité des arbres dans les forêts tempérées et boréales d'Amérique du Nord (Peng *et al.*, 2011).

Les effets des changements climatiques sur les écosystèmes forestiers sont difficiles à anticiper. Bien que les chercheurs aient initialement prédit que les changements climatiques pourraient entraîner une augmentation de la productivité dans les forêts nordiques (Girardin *et al.*, 2016), la hausse des températures peut également limiter la productivité en réduisant la disponibilité en eau du sol étant donné un allongement de la saison de croissance et une augmentation de la demande évaporative de l'atmosphère (Correia *et al.*, 2019 ; Sulman *et al.*, 2016). Avec l'augmentation des épisodes de sécheresse, différentes études prévoient une diminution de la croissance et une augmentation de la mortalité dans les forêts tempérées et boréales du Canada (Correia *et al.*, 2019 ; Girardin *et al.*, 2016 ; Peng *et al.*, 2011).

Les forêts tempérées décidues du sud du Québec sont faces à certains défis. Avec l'augmentation de la température et l'allongement de la saison de croissance, un accroissement de l'évapotranspiration et de l'utilisation de l'eau par les arbres est attendu. De plus, la formation de végétation récalcitrante telle que le hêtre peut également venir modifier le bilan hydrique des peuplements forestiers étant donné le développement progressif d'une dense couche de gaules de hêtre dans le sous-bois. Face à ces problématiques, il est ainsi important de comprendre comment la prolifération du hêtre influence l'utilisation de l'eau par les arbres.

1.4 Objectif de l'étude

L'objectif de cette étude vise à comprendre comment la prolifération du hêtre vient influencer l'utilisation de l'eau par les arbres. À travers des mesures de transpiration par des senseurs de flux de sève, nous avons étudié l'utilisation de l'eau par l'érable à sucre et le hêtre dans des peuplements avec et sans sous-étage dominé par le hêtre.

CHAPITRE 2

INCREASED WATER USE BY SUGAR MAPLE TREES IN THE PRESENCE OF A DENSE BEECH UNDERSTORY LAYER

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Abstract

The formation of a recalcitrant understory vegetation layer is a phenomenon observed in various forests around the world, which can limit tree regeneration and in the long term, modify the composition, succession process and water balance of forests. In temperate forests of southern Quebec (Canada), the proliferation of American beech (*Fagus grandifolia*) in stands dominated by sugar maple (*Acer saccharum*) can be related to the recalcitrant vegetation phenomenon. With a projected increase in the severity and duration of droughts, a better understanding of its effect on water fluxes is crucial to understand the trajectory of impacted forests. The objective of this study was to understand how recalcitrant-type vegetation, in this case beech proliferation in sugar maple stands, influence tree water use. We compared transpiration i) by overstory trees (i.e. sugar maples) and ii) by understory saplings (i.e. American beech) in sites with and without beech understory dominance. At each of the six sites, we measured sap flux density (F_d) of two sugar maple trees (diameter at breast height > 9 cm) and one beech sapling (1 cm < diameter at breat height ≤ 9 cm) with thermal dissipation sensors during the growing season. At tree level, F_d of sugar maple trees was significantly larger in beech-dominated sites compared to control ones, indicating greater water consumption by sugar maple when understory is dominated by beech. At stand scale, total transpiration varied between 140 and 296 mm for the study period, with no significant difference between beech-dominated and control sites. We provide two hypotheses to explain our results at tree scale: i) reduced cover by forest floor vegetation would limit transpiration through this layer, thus allowing increased availability of water resources to supply tree transpiration or ii) increased tree transpiration rate would be a mechanism to satisfy nutrient requirements in beech-dominated stands often associated with lower soil fertility. Further research is needed to better understand the mechanisms explaining tree water use given beech proliferation.

Keywords: *Fagus grandifolia*, *Acer saccharum*, tree water use, recalcitrant understory vegetation, beech understory dominance, sap flux density, transpiration

2.1 Introduction

The formation of a recalcitrant understory vegetation layer is a phenomenon observed in various types of forests around the world (Royo and Carson, 2006). Recalcitrant vegetation typically forms a single-species, dense, persistent, and almost impenetrable layer under the canopy. For example, *Guadua sarcocarpa* Londoño and Peterson, a bamboo specie, has come to dominate the understory of forests in southern Amazonia while the formation of a dense ericaceous shrub layer has been shown to disrupt coniferous regeneration in boreal and temperate forests (Griscom and Ashton, 2003 ; Mallik, 2003). Many recalcitrant species are clonal or thicket-forming species that suppress or largely delay tree species regeneration (Young and Peffer, 2010). In forests, the formation of this recalcitrant vegetation layer can limit tree regeneration and, thus in the long term, modify their composition and the succession process (George and Bazzaz, 1999b ; Royo and Carson, 2006). While the exact cause of the emergence of a recalcitrant vegetation is not always clear, it is often associated with canopy disturbances that increase light availability for the understory layer (Royo and Carson, 2006, 2010).

Recalcitrant understory vegetation can restrict or inhibit regeneration of tree species through various interference mechanisms such as competition for resources (aboveground or belowground), allelopathy (chemical inhibition), litter accumulation on the forest floor, seedling predation by small mammals and mechanical damage (Royo and Carson, 2006). Competition for resources is often cited as one of the main mechanisms through which recalcitrant vegetation interferes with tree regeneration. While various studies have helped gain a better understanding of the role of light competition as an interference mechanism (Beckage *et al.*, 2000 ; Messier *et al.*, 1998 ; Nilsen *et al.*, 2001a), few studies have investigated how recalcitrant vegetation influences the competition for water resources although the formation of a dense understory is likely to modify the partitioning of the forest water balance, and thus tree water use. For example, a dense understory layer could increase interception of precipitation thus reducing the amount of soil moisture and thus plant water availability. In the southern Appalachian mountains, the presence of *Rhododendron maximum* thickets was associated with a 20% reduction in water availability for tree seedlings (Nilsen *et al.*, 2001a). Additionally, a dense understory layer could modify evapotranspiration partitioning in forests, leading to increased understory transpiration. For example, the removal of understory vegetation in thinned forests of western Canada increased soil water availability and resulted in

trees displaying greater rates of photosynthesis (Giuggiola *et al.*, 2018 ; Price *et al.*, 1986). Given a projected increase in the severity and the duration of droughts with climate change (Trenberth *et al.*, 2014), a better understanding of the effects of recalcitrant vegetation on water fluxes is crucial to understand the trajectory of impacted forests under drier conditions.

In temperate forests of southern Quebec (Canada) as well as in eastern North America, the proliferation of American beech (*Fagus grandifolia* Ehrh., hereafter referred to as beech) in stands dominated by sugar maple (*Acer saccharum* Marsh) can be related to the recalcitrant vegetation phenomenon given its impact on sugar maple regeneration. In these stands, sugar maple, the late succession species under mesic conditions (Poulson and Platt, 1996), and beech have co-existed for centuries. However, in the last decades, many studies (Bose *et al.*, 2017 ; Cale *et al.*, 2013 ; Houston, 2001) have reported a dense and almost monospecific understory beech layer, with sometimes more than 1500 beech saplings per hectare in maple-dominated stands (Duchesne *et al.*, 2005 ; Nolet *et al.*, 2008). As a result of the dense understory beech layer, changes in the light regime can negatively affect sugar maple regeneration (Collin *et al.*, 2017). Moreover, beech leaves have a high content of lignin (10% more than sugar maple) (Melillo *et al.*, 1982) and a thick layer of litter often accumulates in beech-dominated stands. This can further interfere with sugar maple regeneration although this interference mechanism has been little studied. The proliferation of beech appears favoured by canopy openings as a result of selective cutting (Nolet *et al.*, 2008 ; St-Jean *et al.*, 2021) and can be further amplified given deer's low browsing preference for beech (Nyland *et al.*, 2006).

A decline in sugar maple and an increase in beech have been noted in southern Quebec (Direction de la recherche forestière, 2017): the density of beech saplings has doubled over a 10-year period in most deciduous forests in Quebec and that of sugar maple has decreased by 20% over the same period (Duchesne *et al.*, 2005). These changes in forest composition are also worrisome given the recent expansion of beech bark disease in the region (Ministère des Forêts, de la Faune et des Parcs, 2020 ; Nolet *et al.*, 2015 ; Roy and Nolet, 2015). This disease is associated with widespread mortality of beech: 20 to 50% of beech trees die during the killing front stage (Ehrlich, 1934 ; Kasson and Livingston, 2012), with mortality mainly concerning mature trees (Roy and Nolet, 2018). Overall, the proliferation of beech in sugar maple stands combined with the high rate of mortality for mature beech trees may shift forests towards mono-specific stands of beech saplings

and poles, with an ensuing impact on the provision of ecosystem services by these forests (e.g. timber supply, habitat, food supply). Given the ecological and socio-economic importance of sugar maple stands in southern Quebec, a better understanding of the impacts of beech proliferation on water fluxes is needed to assess the long-term trajectory of sugar maple stands and to better manage these forests facing a change in composition.

The main objective of this study was to understand how recalcitrant-type vegetation, in this case beech proliferation in sugar maple stands, influence tree water use. More specifically, we compared i) the transpiration of overstory trees (i.e. sugar maples) with and without beech understory dominance and ii) the transpiration of understory saplings (i.e. American beech) with and without beech understory dominance. We hypothesized that the formation of a dense understory beech layer increases competition for water resources thus leading to reduced water use by sugar maple trees in beech-dominated stands. Indeed, beech-dominated stands are characterized by a dense beech sapling strata and water availability is generally negatively correlated with stand density (Brown *et al.*, 2005 ; Scott and Prinsloo, 2008). To test this hypothesis, we measured sap flux density (F_d) as a proxy for tree water use (Flower *et al.*, 2018 ; Grossiord *et al.*, 2014).

2.2   Materials and methods

2.2.1   Study area

This study was conducted in the Kenauk private nature reserve (45.71° to 45.84° N, −74.95° to 74.77° W), in southern Quebec (Canada) that spans 270 km^2 and where mesic forests are dominated by sugar maple along with basswood (Forget *et al.*, 2006). Managed forests, either even-aged or uneven-aged stands, occupy a large portion of the nature reserve. About 50% of the reserve territory is occupied by deciduous forests dominated by red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) (Forget *et al.*, 2006 ; Roux, 2019 ; Varin *et al.*, 2015). Data from the nearest weather station (13 km west from study area) indicate an annual average air temperature of 5.3°C for the 1981-2010 period, ranging from a minimum temperature of –11.2°C in January to a maximum temperature of 19.3°C in July (station 7035666, Environment Canada). Annual average precipitation for the same period was 1204 mm, with precipitation more or less evenly distributed throughout the year.

2.2.2   Experimental design

We selected six sites in uneven-aged stands where the overstory was dominated by sugar maple and the basal area of trees (Diameter at Breast Height (DBH) > 9 cm) greater than 20 m^2 ha^{-1}. Distance between sites varied between 0.7 km to 14.7 km. Among the six sites, we selected three sites where the basal area of beech saplings (1 cm < DBH < 9 cm) was greater than 2 m^2 ha^{-1} (hereafter referred to as beech-dominant sites for brevity), and three sites where the basal area of beech saplings was less than 0.5 m^2 ha^{-1} (hereafter referred to as control sites). A preselection of sites was carried out using data from the 5th forest inventory of the Ministère des Forêts, de la Faune et des Parcs (MFFP) to have sites similar in terms of surface deposition (thin or medium soil thickness), slope classes (gentle to moderate slopes) and drainage classes (good to moderate drainage).

2.2.3   Forest composition and structure

At each site, we recorded the species and DBH of trees in a circular plot with a radius of 25 m. We inventoried saplings in ten subplots with a radius of 2.83 m systematically arranged within the circular plot. We measured the leaf area index (LAI) with a LAI-2000 plant canopy analyzer (LI-COR Inc, USA). The LAI-2000 is composed of two optical sensors (LAI-2500) which were deployed simultaneously: one in an open environment near the measurement site and the second under the canopy at the measurement site. Both sensors were installed at about two meters above the ground. To avoid interference from direct solar radiation, measurements were taken at sunrise. For each site, measurements were taken every 15 seconds for a period of 15 minutes along two perpendicular transects in the center of the plot. The measurements of the two sensors were combined and processed with the FV2000 software. A random distribution of foliage was assumed to compute the LAI.

2.2.4   Meteorological measurements

Within the Kenauk private reserve, a weather station (45.750843° N, -74.825903° W) collected data on air temperature and relative humidity, precipitation, wind speed and direction. The weather station is located in an open environment near a lake. The weather station was located less than 10 km from study sites. At each site, we also measured local air temperature and relative humidity

(RH) using LogTag HAXO-8 sensors (±0.5 °C, ± 3% RH). Sensors were placed in PVC tubes to avoid direct solar radiation and fixed to trees at a height of two meters.

2.2.5 Sap flux measurements

From June to August 2020, we used heat dissipation type sensors (Granier, 1985) to measure the sap flux density of three trees per site: one "small" sugar maple (9 cm < DBH < 20 cm), one "large" sugar maple (DBH > 20 cm) and one beech sapling. The heat dissipation sensors were self-manufactured and made of two cylindrical probes (20 mm length, 2 mm diameter). We removed the bark on trees and inserted probes at breast height, separated by a vertical distance of 10 cm. Probes were installed on the north face of the trunk and inserted in aluminum tubes the same length as the probes to ensure good heat distribution. The probes were then covered by a reflective panel to prevent heating from outside. The probes were connected to an Arduino data logger which recorded data every second and stored 15-minute averages.

The upper probe was heated at constant power and the temperature difference between the two probes is related to sap flux density with the empirical equation developed by Granier (1985):

$$F_d = 119 \times 10^{-4} \times 3600 \; K^{1.231} \tag{1}$$

where F_d is the sap flux density (cm h^{-1}) and K is the dimensionless index of sap flux

$$K = \frac{\Delta T_{max} - \Delta T}{\Delta T} \tag{2}$$

where ΔT_{max} is the maximum temperature difference between the two probes under zero flux conditions (°C) and ΔT is the temperature difference between the two probes under positive sap flow (°C).

We used the R package Aquaflux (Speckman *et al.*, 2020) to analyze data, namely to aid the estimation of ΔT_{max}. ΔT_{max} was computed for each sensor at multiple time points according to several criteria: ΔT_{max} must be a local maximum occurring at night and the vapor pressure deficit (VDP) must be below 0.2 kPa for at least two hours. To evaluate the errors related to the estimation of ΔT_{max}, such as night-time water movement, it was necessary to determine ΔT_{max} at the maximum

point over a period of five consecutive nights (Lu *et al.*, 2004 ; Reyes-García *et al.*, 2012). Giving gaps in data, ΔT_{max} were manually selected according to listed criteria and linearly interpolated to provide a baseline to compute F_d values.

Total sap flow of a given tree was calculated as:

$$Q = F_d\, A \tag{3}$$

where Q is the sap flow (cm^3 h^{-1}), and A is the sapwood area (cm^2). We calculated daily Q by integrating hourly F_d values over daytime (9:00 to 18:00). We estimated the sapwood area using allometric equations derived by Hernandez-Santana et al. (2015) for their study in the White Mountain National Forest, New Hampshire (USA):

$$A = \beta_0 * DBH^{\beta_1} \tag{4}$$

where β_0 and β_1 are species-specific coefficients (β_0 = 0.78 and β_1=1.97 for sugar maple, β_0 = 0.67 and β_1=1.92 for beech).

The total transpiration rate (E_t, cm h^{-1}) at a site was computed as:

$$E_t = \frac{\Sigma_{j=1}^{J} Q_j}{A_g} \tag{5}$$

where J correspond to the total number of trees and saplings at a given site and A_g is the area of the study plot (cm^2). E_t was integrated over time to obtain total transpiration (mm) over the study period (80 days from June 13th and August 31st, 2020). In order to compare total stand transpiration between beech-dominated sites and control ones, we used the linear regression based on the logarithmic relation between VPD and F_d to gap-fill missing data due to sensor failure. To have an estimate of total stand transpiration and as we do not have the sap flux values of the other species found at each site, we assigned i) F_d values of the large sugar maple to all the trees with a DBH greater than 20 cm (regardless of the species), ii) F_d values of the small sugar maple to all trees with a DBH between 9 and 20 cm and iii) F_d of beech saplings to all saplings with a DBH inferior

to 9 cm. While this approach dismisses species-specific transpiration responses to microclimatic conditions (Gebauer *et al.*, 2012 ; Matheny *et al.*, 2014), it allows for a gross estimation of transpiration at the stand scale which is what we aimed for. Indeed, stand-scale transpiration estimates were not the central aspect of the present study but rather computed to provide a general assessment of how measured F_d values would translate into total transpiration at the stand scale. This scaling-up allowed us to validate the flux magnitude in order to compare our results with other transpiration studies in deciduous forests.

2.2.6   Statistical analysis

Using generalized linear mixed models (GLMM) with a normal distribution and a link log function, we fitted a global model where daily Fd was modelled as a function of log (base 10) transformed daily VPD (continuous variable), the level of beech understory dominance (categorical variable with two levels, beech-dominated and control) and the interaction between these two variables. We fitted three independent models for i) large and ii) small sugar maple overstory trees as well as iii) beech saplings in the understory. To avoid issues with few erroneous data, we averaged VPD at the six study sites and use this site-averaged VPD as explanatory variable. When modelling F_d of sugar maple trees, we defined random effects as the day of the year crossed with the tree identifier nested within the site. When modelling Fd of the beech saplings, we defined random effects as the day of the year crossed with the site given only one sapling was sampled per site. All models were fitted by setting control sites as reference and model estimates thus refer to the presence of beech understory dominance. Using the package DHARMa (Hartig *et al.*, 2021), we validated the global model for residual normality and homoscedasticity on the standardized residuals of the model.

We used a model selection approach (Anderson *et al.*, 2000) to assess how the level of beech understory dominance influenced F_d of sugar maple trees and beech saplings. We fitted a suite of candidate models using all possible combinations of the two explanatory variables and we compared models using Akaike's information criterion adjusted for small sample sizes (AIC_c). First, we computed ΔAIC_c for each model, that is the difference in AIC_c between the model and the best candidate model (i.e. with minimum AIC_c). A model with $\Delta AIC_c < 2$ provides strong evidence for the model and, as ΔAIC_c increases, the strength of evidence for a model declines. Second, we computed the Akaike weight (ω) of each candidate model as the ratio between the

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ΔAIC_c of a given model and the sum of ΔAIC_c of all the candidate models (Mazerolle, 2006). The Akaike weight represents the probability of a candidate model being the best among candidate models (Wagenmakers and Farrell, 2004). Third, we performed model-averaging to make inference when multiple models had $\Delta AIC_c < 2$ and thus, no best model could be singled out. In this case, we recomputed the AIC_c and the Akaike weight only for the set of models where the variable beech understory dominance was included. The AIC_c and the Akaike weight were recalculated separately for the main effect (beech understory dominance) and for the interaction between beech understory dominance and VPD. Using these values, we then computed model-averaged estimates and their unconditional standard error (unconditional SE) from which we computed the 95% confidence interval of estimates. When the confidence interval of the estimate excluded 0, the associated variable had a significant effect (Mazerolle, 2006, 2020). All analyses were performed with the R software (R Development Core Team, 2010) and we performed model selection and multi-model estimate averages with the AICcmodavg package (Mazerolle, 2020).

2.3 Results

2.3.1 Vegetation density, structure, and composition

Total tree basal area varied between 26.1 m^2 ha^{-1} and 29.1 m^2 ha^{-1} among the six study sites (Table 2.1), with no significant difference in mean tree basal area between the beech-dominated and control sites (t-test, t= 0.23, 4 d.f., p= 0.83). Tree species composition was also similar between beech-dominated and control sites, with sugar maple being the dominant species (41 to 88% of tree basal area, Table 2.1), except for site B2 where sugar maple represented only 12 % of tree basal area. At this site, vegetation was dominated by Canadian hemlock (*Tsuga Canadensis*) and beech which respectively accounted for 40% and 34% of tree basal area. Similar to total tree basal area, mean sapling basal area did not differ between beech-dominated and control sites (t-test, t= 1.66, 4 d.f., p= 0.17). However, species composition of saplings differed between beech-dominated and control sites, with beech saplings covering between 2.1 and 3.2 m^2 ha^{-1} at beech-dominated sites as opposed to covering between 0.0 and 0.4 m^2 ha^{-1} at control sites (Table 2.1). At control sites, the sapling layer was dominated by sugar maple (respectively 77%, 38% and 59% of total sapling basal area for C1, C2 and C3). Mean LAI was also significantly different between beech-dominated and control sites (t-test, t= 3.04, 4 d.f., p<0.05), with mean LAI at beech-dominated sites (5.1 m^2 m^{-2}) being 24% greater than at control sites (4.0 m^2 m^{-2}). Given that tree and sapling basal area did not

differ between beech-dominated and control sites, the observed difference in LAI between sites is likely explained by the dominance of beech in the sapling layer. Indeed, we found a strong correlation between total sapling basal area and LAI (R= 0.92) while correlation between total tree basal area and LAI was weak (R = 0.32).

Table 2.1: Forest density, composition, and structure at study sites. Sites labelled as B correspond to beech-dominated sites while sites labelled as C correspond to control sites. LAI refers to the leaf area index.

Site	Total tree basal area (m^2 ha^{-1})	Sugar maple tree basal area (m^2 ha^{-1})	Beech tree basal area (m^2 ha^{-1})	Other tree species basal area (m^2 ha^{-1})	Total sapling basal area (m^2 ha^{-1})	Beech sapling basal area (m^2 ha^{-1})	LAI (m^2 m^{-2})
B1	26.4	21.6	1.5	3.3	3.7	2.1	5.0
B2	28.3	3.5	9.6	15.2	4.3	3.2	5.6
B3	28.5	11.8	8.9	7.8	2.4	2.3	4.7
C1	26.1	13.6	0.0	12.4	2.5	0.0	3.9
C2	29.1	25.5	0.0	3.6	2.9	0.1	4.4
C3	27.2	23.0	1.5	2.8	1.3	0.4	3.7

2.3.2 Meteorological conditions

During the study period, from June to August 2020, mean air temperature was 19.1 °C and total precipitation was 250 mm at the Kenauk weather station. At the nearest station with long-term data (13 km, station 7035110, Environment Canada), the summer 2020 was relatively warm and wet compared to the climate normal. At this station, mean air temperature in July 2020 was 2.6 °C above the long term 1981-2010 average while mean air temperature in August 2020 was very close to the climate normal. Total precipitation in July and August 2020 were 46 mm above the long-term 1981-2010 average for these two months.

Local air temperature and relative humidity showed little variation between study sites. During the summer 2020, mean air temperature varied between 19.1 and 19.6 °C (ANOVA, p-value = 0.96) at study sites while mean relative humidity varied between 80.3 and 83.3% (ANOVA, p-value = 0.44). Mean VPD varied between 0.4 kPa and 0.5 kPa at study sites and there was no significant difference in mean VPD between the six sites, whether beech-dominated or not (ANOVA, p-value = 0.45).

2.3.3 Effect of VPD and beech understory dominance on F_d of overstory trees

In July and August 2020, daily F_d of sugar maple trees varied between 1.8 and 20.5 cm h^{-1} for the large size class and between 3.2 and 44.8 cm h^{-1} for the small size class (Figure 2.1a-b). As shown in Figure 2.1, F_d increased with VPD, with maximum F_d values associated with drier air conditions. F_d has a logarithmic relationship with VPD: below 0.8 kPa, F_d increased linearly with VPD, and the relationship plateaued beyond that point.

Maximum values of F_d for sugar maple trees were found at beech-dominated sites. For example, F_d greater than 25 cm h^{-1} was only measured in small sugar maples of beech-dominated sites while F_d remained below 20 cm h^{-1} at control sites (Figure 2.1b). We did not measure F_d greater than 25 cm h^{-1} in large sugar maples and F_d remained below 20 cm h^{-1} at both beech-dominated and control sites (Figure 2.1a). For small sugar maples, F_d greater than 25 cm h^{-1} was not a site-wide pattern and such large values only occurred at certain beech-dominated sites. Figure 2.2 shows site-specific relationships between F_d and VPD. Although the tree identifier nested with the site was defined as a random effect in the GLMM, we chose to illustrate site-specific relationships given considerable variability from site to site. For example, maximum F_d of small sugar maples was observed at the beech-dominated site B2 with F_d generally varying between 25 and 40 cm h^{-1} (Figure 2.2b) while F_d was generally below 20 cm h^{-1} at beech-dominated site B3 (Figure 2.2c) or at control sites (Figure 2.2d-f). Large F_d values were also observed at beech-dominated site B1 where F_d exceeded 20 cm h^{-1} for VPD > 0.8 kPa (Figure 2.2a).
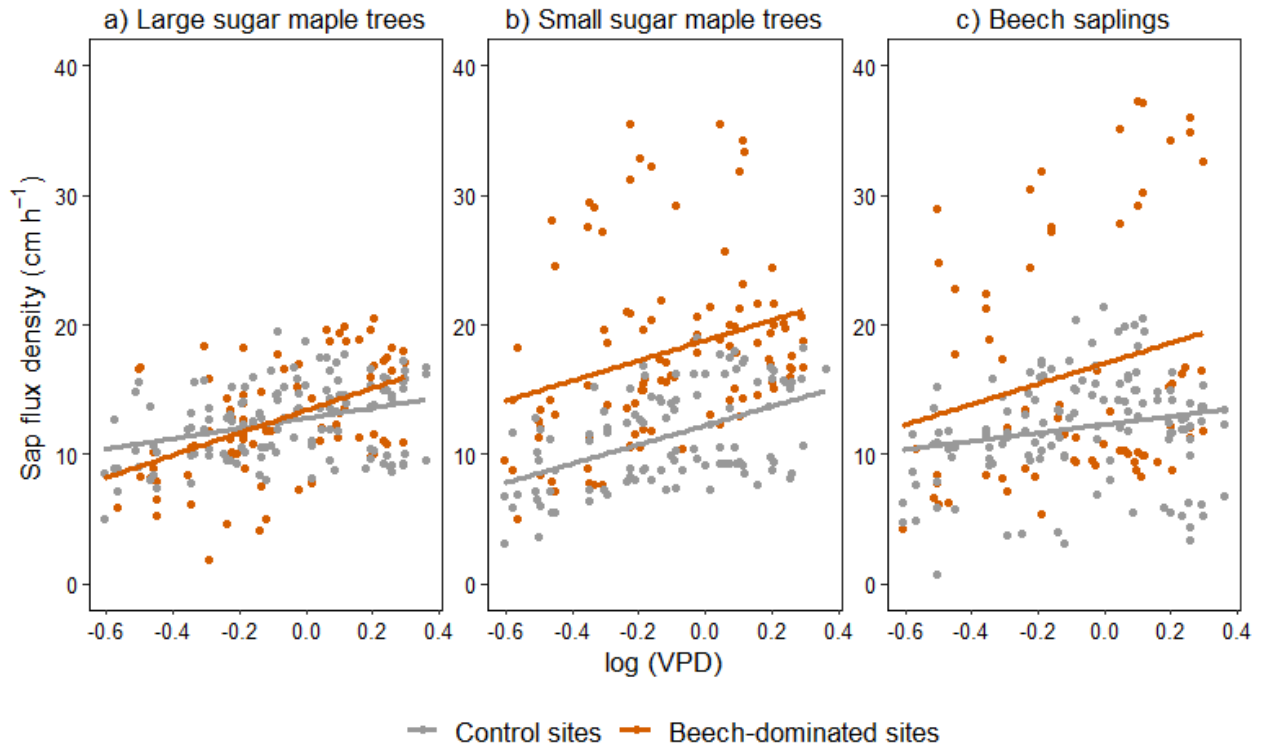
Figure 2.1 : Relationship between sap flux density (F_d, cm h^{-1}) and log-transformed (base = 10) vapor pressure deficit (VPD, kPa) for a) large sugar maple trees (DBH > 20 cm; n = 3), b) small sugar maple trees (9 cm < DBH < 20 cm; n = 3 and c) American beech saplings (1 cm < DBH < 9 cm; n = 3) at beech-dominated sites and control sites.

Model selection suggests that the effect of the beech understory dominance on F_d of sugar maple varied between size classes (Table 2.2). When modelling F_d of small and large sugar maple, model diagnostic indicated adequate fit for the global model (model 1.1, model 2.1 in Table 2.2, see Figure S1-S2). For large sugar maple trees, the effect of beech understory dominance on F_d was weak (Figure 2.1a) as confirmed by the relatively low Akaike weights ($0.00 \leq \omega \leq 0.32$, Table 2.2) of candidate models that include beech understory dominance as an explanatory variable (models 1.1, 1.2, 1.4, 1.5). The model with VPD alone (model 1.3) has the greatest probability (56%) of explaining the variation in daily F_d (Table 2.2). Still, multimodel inference suggests a significant positive effect for the interaction between beech understory dominance and VPD with a model-averaged estimate ranging between 0.27 and 1.01 (Table 2.3). Indeed, the F_d of large sugar maple trees was slightly greater for beech-dominated sites than control ones under dry atmospheric conditions (VPD > 0.8 kPa, Figure 2.1).

Figure 2.2: Relationship between sap flux density (F_d, cm h^{-1}) and log-transformed (base = 10) vapor pressure deficit (VPD, kPa) for beech-dominated sites (a,b and c) and control sites (d, e and f) for sugar maple trees (small: $9 < DBH < 20$ cm, large: $DBH > 20$ cm) and beech saplings (DBH < 9 cm).

In contrast, F_d of small sugar maple trees was overall greater in beech-dominated sites than in control sites (Figure 2.1b) and model selection clearly indicates the inclusion of beech understory dominance as a variable of the best model (model 2.2, Table 2.2). For small sugar maple trees, the model with VPD and beech understory dominance as main effects had the greatest Akaike weight (model 2.2, $\omega = 0.57$) among candidate models. Multimodel inference indicates that beech understory dominance significantly influenced daily F_d, with a model-averaged estimate ranging between 0.04 and 1.07 for beech understory dominance as a main effect (Table 2.3). In summary, compared to control sites, F_d of small sugar maple trees was overall superior at beech dominated sites while F_d of large sugar maple trees was only superior at beech dominated sites under dry atmospheric conditions (VPD > 0.8 kPa).

Table 2.2: AICc of generalized linear mixed models of daily sap flux density of large sugar maple trees, small sugar maple trees and beech saplings. The symbol * indicates the interaction between two variables, the symbol + indicates the combination of variables and the symbol : indicates only the interaction between two variables.

Model number	Model	Number of parameters	AICc	ΔAICc	Akaike weight (ω)
	Large sugar maple trees				
1.1	Log (VPD) * Beech understory dominance	9	869.6	5.1	0.04
1.2	Log (VPD) + Beech understory dominance	8	868.5	3.9	0.08
1.3	Log (VPD)	7	864.5	0.0	0.56
1.4	Beech understory dominance	7	919.4	54.8	0.00
1.5	Log (VPD) : Beech understory dominance	8	865.7	1.1	0.32
1.6	Intercept	6	915.2	50.7	0.00
	Small sugar maple trees				
2.1	Log (VPD) * Beech understory dominance	9	880.1	5.7	0.03
2.2	Log (VPD) + Beech understory dominance	8	874.3	0.0	0.57
2.3	Log (VPD)	7	875.1	0.8	0.38
2.4	Beech understory dominance	7	945.3	70.8	0.00
2.5	Log (VPD) : Beech understory dominance	8	880.8	6.5	0.02
2.6	Intercept	6	945.8	71.5	0.00
	Beech saplings				
3.1	Log (VPD) * Beech understory dominance	9	867.5	2.2	0.14
3.2	Log (VPD) + Beech understory dominance	8	865.3	0.0	0.41
3.3	Log (VPD)	7	865.7	0.0	0.34
3.4	Beech understory dominance	7	929.5	64.2	0.00
3.5	Log (VPD) : Beech understory dominance	8	867.8	2.5	0.12
3.6	Intercept	6	929.8	64.5	0.00

Table 2.3: AICc and associated measures recomputed to obtain model-averaged estimates and standard error associated with the level of beech understory dominance.

Model	**Variable**	**Model-averaged estimate**	**Unconditional standard error**	**95% Unconditional confidence interval**
Large sugar maple trees	Beech understory dominance	0.05	0.16	-0.27, 0.37
	Beech understory dominance*log (VPD)	0.64	0.19	**0.27, 1.01**
Small sugar maple trees	Beech understory dominance	0.55	0.26	**0.04, 1.07**

	Beech understory dominance*log (VPD)	0.33	0.38	-0.41, 1.08
Beech saplings	Beech understory dominance	0.70	0.45	-0.19, 1.59
	Beech understory dominance*log(VPD)	0.23	0.41	-0.56, 1.03

2.3.4 Effect of VPD and beech understory dominance on F_d of understory saplings

Similar to sugar maple trees, the F_d of beech saplings increased with VPD and daily F_d varied between 0.7 and 43.5 cm h^{-1} during the study period (Figure 2.1c). Similar to small sugar maples, maximum F_d of beech saplings was measured at beech-dominated sites but large values (> 25 cm h^{-1}) were not observed at all beech-dominated sites. For example, F_d values generally varied between 20 and 40 cm h^{-1} at sites B1 and B3 (Figure 2.2a, c) while they remained below 20 cm h^{-1} at site B2 (Figure 2.2b) as well as at all control sites (Figure 2.2d-f).

For beech saplings, we must emphasize that no model fit could be found to satisfy normally distributed residuals, even after various attempts (Figure S3). Consequently, Akaike weights and multi-model inference should be taken with caution. Combined with log-transformed VPD, beech understory dominance was included in the best model with an Akaike weight of 0.41 (model 3.2, in Table 2.2). According to multimodel inference, beech understory dominance had no significant effect on F_d of beech saplings. Indeed, the model-averaged estimate varied between to -0.19 to 1.59 for the main effect and between -0.56 to 1.03 for the interaction between beech understory dominance and VPD (Table 2.3).

2.3.5 Effect of beech understory dominance on total stand transpiration

For the study period (n = 80 days), total transpiration (overstory and understory) varied between 241 and 296 mm for beech-dominated sites and between 140 and 269 mm for control sites (Figure 2.3). Control site C1 had the lowest transpiration (140 mm) as a result of relatively small F_d values (< 10 cm h^{-1}) for all size classes (Figure 2.2d). On average, transpiration by the understory layer represented 11% of total stand transpiration. Transpiration by the understory layer at beech-dominated sites (25-57 mm) was two to three times greater than at the control sites (8 to 22 mm)

and represented 15% of total stand transpiration as opposed to 7% at control sites. Transpiration by the overstory layer was dominated by trees of the small size class, which accounted for 8 to 36% of total stand transpiration at study sites while trees of the large size class contributed between 6 and 20% to total stand transpiration.

Total stand transpiration (understory and overstory) was not significantly different between beech-dominated and control sites (ANOVA, p-value = 0.17). When looking at each size class, mean transpiration of large trees (ANOVA, p-value = 0.76), small trees (ANOVA, p-value = 0.25) and saplings (ANOVA, p-value = 0.08) were not significantly different between beech-dominated and control sites. This can be explained by the fact that the scaling up of F_d as a function of sapwood area (equation 3) was similar between sites given that overstory and understory basal area were not significantly different between beech-dominated and control sites (Table 2.1). As such, greater tree F_d associated with beech understory dominance appeared overridden by the scaling up process, leading to similar values of total transpiration at beech-dominated and control sites.
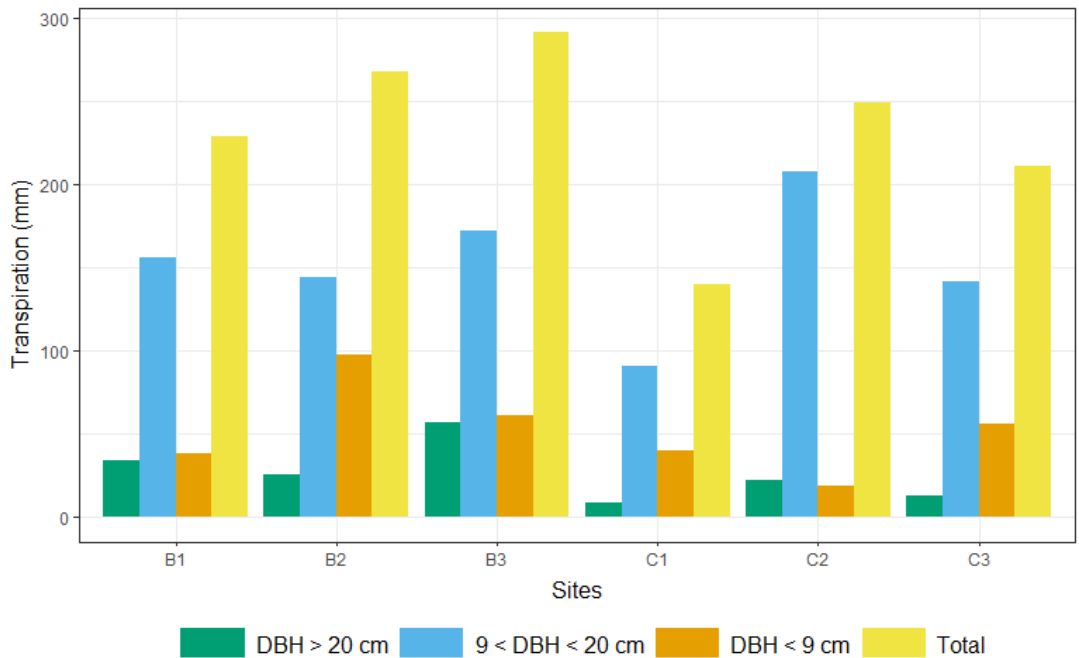

Figure 2.3: Total transpiration from June 13th to August 31st, 2020 (n = 80 days) for beech-dominated (B1-B3) and control (C1-C3) sites partitioned into three DBH classes, i.e. large tree (DBH > 20 cm), small trees (9 < DBH < 20 cm) and saplings (DBH < 9 cm).

2.4   Discussion

2.4.1   Increased water use in overstory trees of beech-dominated sites

We had hypothesized that, with the formation of a dense understory beech layer, overstory trees would face greater competition for water resources thus having reduced water use. In line with this hypothesis, we expected F_d of overstory trees to be lower in beech-dominated sites than in control sites. Contrary to our hypothesis, F_d of sugar maple trees was greater at beech-dominated sites than at control sites, especially for trees of the small size class and under relatively dry atmospheric conditions (VPD > 0.8 kPa, Figure 2.1a-b). We provide two potential, albeit contrasting, hypotheses to explain the greater F_d of overstory trees in beech-dominated stands.

On the one hand, the greater F_d of sugar maple trees in beech-dominated stands could suggest a greater availability of water resources and thus reduced competition compared to control sites. This greater availability of water could potentially be explained by the presence of a thick layer of litter at beech-dominated sites that may hinder the development of forest floor vegetation. Indeed, reduced cover by forest floor vegetation has been found in the presence of dense beech thickets in eastern North America (Cale *et al.*, 2013). Consequently, a reduction in forest floor vegetation could free up water resources for overstory trees thus leading to greater tree F_d in beech-dominated stands. Indeed, decomposition of beech leaves is slow due to their high lignin content (Melillo *et al.*, 1982). Thus, leaves accumulate over time and form a thick layer of litter. This thick layer limits light availability for seedlings and ground vegetation, preventing the regeneration of many species (Cale *et al.*, 2013 ; Hane, 2003 ; Nyland *et al.*, 2006). Furthermore, beech leaf has a phytotoxic component which can inhibit the regeneration of sugar maple (Hane *et al.*, 2003). Thus, the development of forest floor vegetation is often limited in beech-dominated stands, although we did not assess this at our sites. The hypothesis that water resources are freed up by the absence of forest floor vegetation is supported by the fact that transpiration by this vegetation layer can represent a considerable fraction of stand-scale evapotranspiration (Gobin *et al.*, 2015). According to studies in temperate forests, forest floor transpiration accounts for 10 to 15% of total evapotranspiration for closed-canopy forests with sparse forest floor vegetation, and it can reach up to 40% in more open forests (LAI < 3) (Landuyt *et al.*, 2019 ; Oishi *et al.*, 2018). Overall, a better understanding of evapotranspiration at the forest floor is needed to assess its influence on the water budget of beech-dominated sites.

On the other hand, transpiration powers the movement of nutrients and the greater F_d observed in beech dominated stands may indicate different nutrient status between beech-dominated and control sites. As such, beech-dominated sites may be poorer in terms of nutrients leading to trees requiring more water to sustain their nutrient requirements, thus explaining greater F_d rates. During the present study, water, as opposed to nutrients, was perhaps not an important limiting factor as precipitations were slightly above the climatic normal, with 46 mm above the 1981-2010 long-term average. Instead, many studies have shown that stands dominated by beech saplings are associated with soils of lower fertility which could be due to the fact that beech outcompetes sugar maple in less fertile sites (Hane *et al.*, 2003 ; Kobe *et al.*, 2002) or that beech litter is very acid and lowers soil fertility (Côté and Fyles, 1994). Various studies have shown increased rates of transpiration by trees in soils of low fertility (Cramer *et al.*, 2008 ; Matimati *et al.*, 2014). For example, fertilization of hardwood forests with municipal solid waste translated into reduced transpiration rate for sugar maple and American beech (Gordon *et al.*, 1989). As such, nutrient limitations could potentially explain the greater F_d in beech-dominated stands compared to the control ones. Overall, we offered here two alternative explanations to observed patterns of F_d in beech-dominated and further work should aim to gain a better understanding of foremost limiting factors (water vs nutrient) when a dense beech understory layer develops in sugar maple stands.

2.4.2 Undetermined effect of beech understory dominance on water use by understory vegetation

In the absence of proper model fit, results were inconclusive as for the influence of beech understory dominance on the water use by understory beech saplings. Still, the largest F_d measured in beech saplings occurred at beech-dominated sites (Figure 2.2a, c), in line with our finding that F_d of overstory trees was greater at beech-dominated sites. Regarding the F_d of beech saplings, we observed considerable variability between beech-dominated sites which could stem from various sources. First, beech is known for its capacity to regenerate either from sprouts or from seedlings (Nyland *et al.*, 2006 ; Wagner *et al.*, 2010 ; Ward, 1961). These two different types of regeneration likely involve different root systems for beech, which could influence patterns of water use. Hence, the consideration of the beech regeneration mode, which was outside the scope of this study, could help explain pattern of F_d in beech saplings. Second, while site selection was carried out to have similar conditions in terms of slope, soil thickness and drainage, site-level variability at beech-

dominated sites could be linked to an abiotic variable not measured such as nutrient concentrations. Although this study involved a considerable field sampling effort in line with other studies monitoring F_d in natural forests, the sample size (one sapling per site and three sites per treatment) was relatively small. Increasing the sample size would improve our ability to compare the water use of beech saplings with or without beech understory dominance.

2.4.3   Total stand transpiration is comparable at beech-dominated and control sites

At all sites (beech-dominated or control), total stand transpiration (sum of transpiration by understory and overstory vegetation) varied between 140 and 296 mm for the period going from mid-June to the end of August (Figure 2.3). This is a gross estimation of total stand transpiration knowing that the scaling-up approach disregards all species-specific F_d. In a North American deciduous forest, Wullschleger *et al.*(2001) reported total transpiration that reached 267 mm during the growing season, with 83% of transpiration from overstory trees and 17% from understory saplings. We found a similar partitioning of transpiration with understory vegetation amounting to 10 to 20% of total transpiration at beech-dominated sites and 6 to 9% at control sites. Total transpiration by overstory trees varied between 131 and 242 mm during the study period, which correspond to an average transpiration rate of 1.6 and 3.0 mm day^{-1}. Despite the limitations of this scaling-up analysis (see methodology), these results are in line with the literature as the average daily transpiration rate has been found to vary between 1 and 5 mm day^{-1} in sugar maple stands of northeastern America (Bernier *et al.*, 2002 ; Collins *et al.*, 2018 ; Ewers *et al.*, 2008).

Although maximum values of total stand transpiration were found in beech-dominated sites, we found no significant differences between the average transpiration of beech-dominated and control sites. Likewise, we found no significant differences for understory and overstory transpiration. This can be explained by the fact that the scaling up of F_d is a function of sapwood area (equation (3). Indeed, overstory and understory basal area were not significantly different between beech-dominated and control sites (Table 2.1). As such, greater tree F_d associated with beech understory dominance appeared overridden by the scaling up process, leading to similar values of total transpiration at beech-dominated and control sites.

2.4.4 Limitations of the study

First, we used the original Granier calibration for the calculation of F_d (equation 1) which could influence estimates of water use on an absolute level. For diffuse-porous species like American beech, calibration experiments normally agreed with Granier's calibration (Bush *et al.*, 2010), although Steppe *et al.*(2010) found there was an underestimation of F_d of 60% when using the original calibration for American beech. Still, this study largely focused on a comparison of water use between trees of the same species and as such, the use on a relative level of the original Granier calibration appeared appropriate to assess the influence of beech understory dominance on F_d. Second, this study computed only a gross estimate of total stand transpiration, which could be improved with measurements of F_d in other tree species. Indeed, we assigned F_d values of sugar maples to all trees (DBH > 9 cm) inventoried at a given site. This assumption appeared reasonable given that sugar maple represented between 41 and 88% of the tree basal area (except site B2, Table 2.1), although monitoring additional tree species would improve estimates of absolute water use at the stand-scale. Similarly, F_d was only measured in beech saplings and these values were assigned to all saplings inventoried at a given site. While this assumption was largely reasonable at beech-dominated sites where beech represented between 57 and 96% of sapling basal area, F_d measurement in sugar maple saplings would improve estimates of stand-scale absolute water use at control sites where sugar maple could make up to 77% of the sapling basal area (Table 2.1). Considering a single species for the stand-scale transpiration estimate can lead to uncertainties, it is indicated by high coefficients of variation (29-33% in Gebauer *et al.*, 2012).

2.4.5 Conclusion

Using thermal dissipation sensors, this study measured F_d in overstory trees (i.e. sugar maple) and understory sapling (i.e. beech) to assess how the proliferation of beech in the understory of sugar maple stands influenced water use. Contrary to our hypothesis that overstory trees in beech-dominated stands would face increased competition for water resources and thus reduced tree water use, we found that beech understory dominance in sugar maple stands led to an increase in overstory trees water use. We provided two potential explanations to this phenomenon: i) increased availability of water resources in beech-dominated stands given limited transpiration by forest floor vegetation and ii) increased transpiration rates to satisfy nutrient requirements in beech-dominated stands often associated with lower soil fertility. Further research is needed to describe the effect of

beech understory dominance on various hydrological processes, including forest floor evaporation. Such research would be necessary to better apprehend the effect of recalcitrant vegetation on the overall water budget of forests and thus understand its consequences on soil water availability. Moreover, a better understanding of the effect of nutrient limitations on transpiration is also needed and appears particularly important given widespread nutrient deficiencies in sugar maple stands of northeastern America (Côté and Fyles, 1994).

CHAPITRE 3
CONCLUSION GÉNÉRALE

Le présent projet avait pour but de comprendre comment la prolifération par le hêtre, un phénomène s'apparentant à la végétation récalcitrante de sous-bois, influence l'utilisation de l'eau par les arbres dans les forêts décidues du sud du Québec. Il est connu que l'établissement de végétation récalcitrante interfère dans la régénération de certaines espèces d'arbres. Alors que plusieurs études ont étudié la compétition pour la lumière comme mécanisme d'interférence dans la partie aérienne (notamment la compétition pour la lumière), notre étude aborde une lacune dans nos connaissances en étudiant la compétition dans la partie souterraine, c'est-à-dire la compétition pour l'eau. Pour cela, nous avons mesuré et comparé la transpiration d'érables à sucre matures et des gaules de hêtre au sein de peuplements avec et sans sous-étage dominé par le hêtre. Les données d'inventaire effectuées dans les peuplements échantillonnés ont permis de constater des densités de gaules de hêtre plus grandes dans certains sites par rapport à d'autres et de conclure que ces sites sont dominés par le hêtre. Nos résultats montrent que l'utilisation de l'eau par les érables à sucre, tel qu'évalué à partir de mesures de la densité de flux de sève, était supérieure dans les sites avec un sous-étage dominé par le hêtre. Dans un premier temps, une végétation au sol de plus faible densité dans les sites dominés par le hêtre pourrait expliquer l'utilisation accrue en eau par l'érable. En effet, la végétation au sol contribue de manière importante à l'évapotranspiration forestière et une présence moindre de végétation au sol pourrait libérer des ressources hydriques pour les arbres. Dans un deuxième temps, l'appauvrissement en éléments nutritifs associés aux peuplements dominés par le hêtre pourrait également expliquer le fait que l'érable à sucre a une consommation en eau plus importante pour combler ses besoins en éléments nutritifs. Des recherches supplémentaires sont nécessaires afin d'évaluer ces hypothèses.

À l'échelle du peuplement, nous n'avons pas observé de différence significative entre la transpiration des peuplements dominés ou non-dominés par les gaules de hêtre en sous-étage. En effet, une densité de flux de sève plus élevée associée aux arbres dans les sites dominés par le hêtre est outrepassée par la mise à l'échelle, conduisant ainsi à des valeurs similaires de transpiration pour les sites dominés par le hêtre et les sites témoins. Par ailleurs, les valeurs de transpiration dans

nos sites d'étude correspondent aux données de transpiration dans les forêts tempérées dans la littérature.

Ce projet sert de premier pas vers une meilleure compréhension des effets de la prolifération du hêtre sur l'utilisation de l'eau par les arbres et des études subséquentes sont nécessaires pour comprendre les mécanismes à l'œuvre. Tout d'abord, nous avons observé une forte variabilité dans les taux d'utilisation de l'eau entre les arbres et entre les sites. L'échantillonnage d'un plus grand nombre de sites et d'arbres à l'intérieur de ceux-ci serait souhaitable pour faciliter la comparaison des sites. À l'origine, un plus grand effort d'échantillonnage était prévu mais des problèmes d'approvisionnement en matériel associé à la pandémie de COVID-19 nous ont amenés à réviser notre effort d'échantillonnage à la baisse. Cela étant dit, plusieurs études sur la transpiration des arbres ont un effort d'échantillonnage semblable à celui effectué dans le cadre du présent mémoire (par exemple : Pappas et al., 2018 ; Peters et al., 2018). La présente étude a effectué un effort d'échantillonnage rarement atteint dans le suivi de la transpiration de la forêt tempérée québécoise, permettant ainsi de mieux cerner l'ampleur de la variabilité et d'informer de prochaines campagnes de collecte de données. Par ailleurs, la présente étude a permis de cibler certaines variables qu'il serait judicieux de suivre pour mieux comprendre l'influence de la prolifération du hêtre sur les flux hydrologiques, soit l'humidité du sol, l'évapotranspiration par la végétation au sol et les concentrations en éléments nutritifs du sol. Dus à des problèmes liés aux senseurs d'humidité du sol, nous n'avons pas pu collecter ces données. Ce projet de recherche a permis la première évaluation de la transpiration des arbres dans des peuplements dominés par des gaules de hêtre en sous-étage et fournit de nombreuses pistes à explorer pour comprendre les mécanismes régissant l'utilisation de l'eau dans ces peuplements.

ANNEXE A

SUPPLEMENTARY MATERIALS

Figure S1: Validation of the model for large sugar maple trees. Left panel: qq-plot with correct distribution (KS test), dispersion and outliers. Right panel: plot of the residuals against the predicted value.
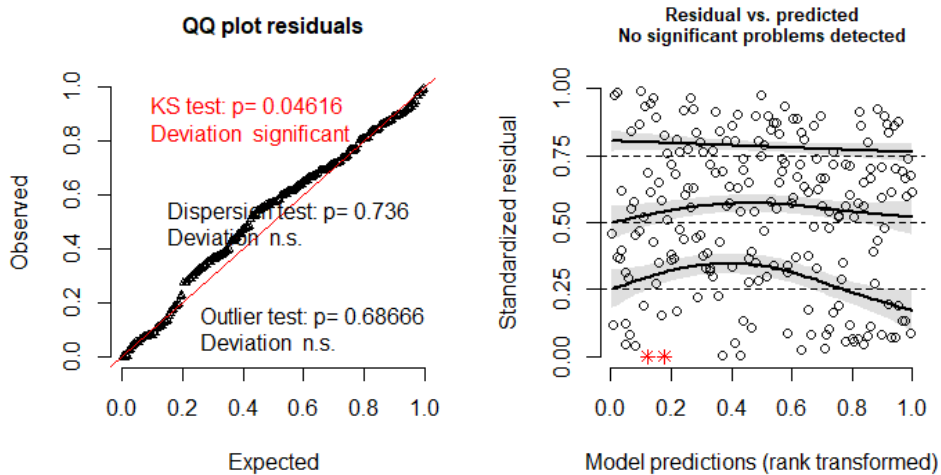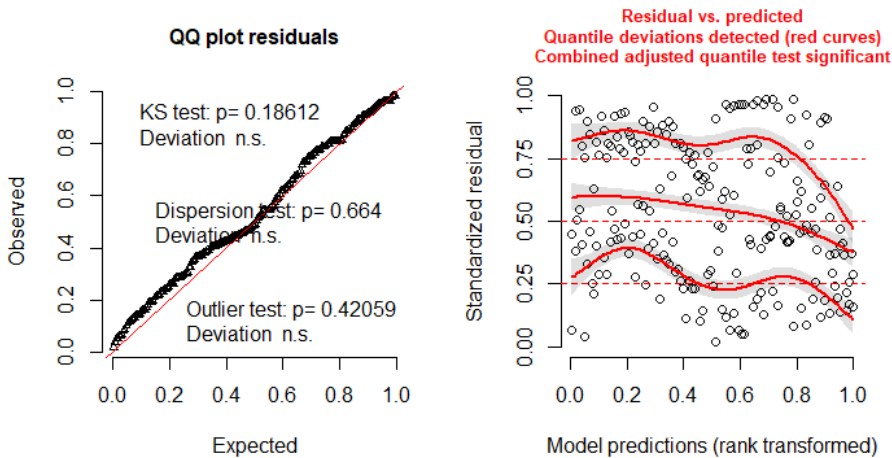

Figure S2: Validation of the model for small sugar maple trees. Left panel: qq-plot with correct distribution (KS test), dispersion and outliers. Right panel: plot of the residuals against the predicted value.
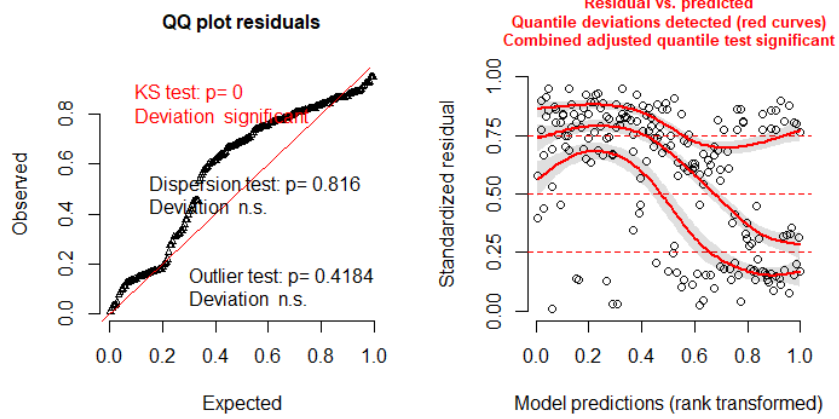
Figure S3: Validation of the model for beech saplings. Left panel: qq-plot with correct distribution (KS test), dispersion and outliers. Right panel: plot of the residuals against the predicted value.

MEASURED TREES IDENTIFICATION AND DBH

Tableau S1: Studied trees location, identification, species and DBH for F_d measurements

Site	Tree ID	Species	DBH (cm)
B1	B11	Sugar maple	41
B1	B12	Sugar maple	24,2
B1	B13	American beech	6,7
B2	B21	Sugar maple	32
B2	B22	Sugar maple	18,1
B2	B23	American beech	7,2
B3	B31	Sugar maple	34,6
B3	B32	Sugar maple	12,5
B3	B33	American beech	7,4
C1	C11	Sugar maple	37,8
C1	C12	Sugar maple	11,8
C1	C13	American beech	6,6
C2	C21	Sugar maple	27,7
C2	C22	Sugar maple	10
C2	C23	American beech	6,7
C3	C31	Sugar maple	26,6
C3	C32	Sugar maple	21,2
C3	C33	American beech	6,5

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