UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFET À COURT TERME DE L'ÉCLAIRCIE SUR LA TRANSPIRATION DE L'ÉRABLE ROUGE EN FORÊT MIXTE TEMPÉRÉE

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A	Sapwood area
BA	Basal area
cm	Centimeter
DBH	Diameter at breast height
Et	Transpiration rate
Fd	Sap flux density
GLMM	Generalized linear mixed models
h	Hours
ha	Hectare
K	Dimensionless index of sap flux
kPa	Kilopascal
LAI	Leaf Area Index
m	Meter
Q	Sap flow
VPD	Vapor pressure deficit

RÉSUMÉ

Les projections climatiques futures montrent que les forêts vont subir davantage d'événements secs extrêmes pouvant accroître la mortalité des arbres. Des pratiques de sylviculture, telles que l'éclaircie, ont été utilisées pour réduire la compétition pour l'eau et ainsi accroître la résistance des forêts face à des sécheresses. L'efficacité de l'éclaircie a été largement démontrée sous des conditions climatiques semi-arides. Toutefois, il existe peu d'information sur la réponse des forêts tempérées ainsi que la surface terrière residuelle requise pour en retirer des bénéfices. Ce projet vise à comprendre comment des éclaircies créant un gradient de surfaces terrières résiduelles affectent la transpiration de peuplements forestiers dominés par l'érable rouge (*Acer rubrum*) dans le sud du Canada. Nous avons mesuré la densité de flux de sève (Fd) à l'aide de capteurs de dissipation thermique pour 18 érables rouges répartis sur neuf parcelles expérimentales éclaircies afin d'obtenir un gradient de surface terrière résiduelle (20 ; 12,5 ; et 6 m^2 ha^{-1}). Durant la première saison de croissance après les traitements, les parcelles avec une faible surface terrière résiduelle (6 m^2 ha^{-1}) ont eu des conditions atmosphériques plus sèches du fait d'un déficit de tension de vapeur (VPD) significativement plus important que dans les parcelles avec une grande surface terrière résiduelle (20 m^2 ha^{-1}). À l'échelle de l'arbre, le Fd a augmenté avec la surface terrière résiduelle, avec les différences les plus marquées entre les traitements pour des conditions atmosphériques sèches. Quand le VPD journalier excédait 1,1 kPa, le Fd moyen des parcelles avec une grande surface terrière résiduelle était respectivement 20 % et 75 % plus important que dans les parcelles avec une surface terrière résiduelle moyenne (12.5 m^2 ha^{-1}) et faible. De plus, nous avons trouvé une forte variabilité de la réponse de Fd au niveau du site dépendamment du traitement de surface terrière résiduelle. Au niveau du peuplement, la transpiration totale simulée pour des parcelles avec une surface terrière résiduelle faible et moyenne correspondait à 41 % et 79 % de la transpiration simulée pour une parcelle avec une grande surface terrière résiduelle. Ainsi, ce travail a mis en lumière la grande variabilité des forêts tempérées en réponse à des traitements d'éclaircie, soulignant la nécessité d'une meilleure modélisation du bilan hydrique des forêts et du partitionnement de l'évapotranspiration de la strate arborée et de sous-étage afin de prescrire des surfaces terrières adéquates en forêt tempérée.

Mots clés : densité de flux de sève, surface terrière résiduelle, transpiration, érable rouge, déficit de tension de vapeur, hydrologie

CHAPITRE I

INTRODUCTION

1.1 Problématique

Les changements climatiques, résultant d'une augmentation des émissions de gaz à effet de serre, sont devenus une préoccupation majeure au fil des ans. L'ensemble des régions du globe sont touchées et voient leur climat modifié. Une augmentation de l'intensité des épisodes de sécheresse est notamment prévue à l'échelle globale (Dai, 2013). Au Québec, une augmentation des températures est projetée avec pour conséquence, la modification du régime de précipitations et la multiplication des vagues de chaleur (Ouranos, 2015). La hausse des températures a pour conséquence d'augmenter la demande évaporative de l'atmosphère, ce qui, en climat tempéré humide, se traduirait par une hausse du taux de transpiration des arbres et une diminution de la disponibilité en eau du sol. Le stress hydrique peut mener à une diminution de la croissance des arbres et une augmentation de leur mortalité (Allen et al., 2010). Un exemple marquant au Canada est l'impact de la sécheresse de 2001 et 2002 sur les populations de peuplier faux-tremble (*Populus tremuloides*) dans les savanes boréales, bordant le nord des prairies des provinces centrales du Canada, qui ont vu leur taux de mortalité augmenter de près de 35 % et leur croissance diamétrale réduire de 30 % suite à cet événement (Hogg et al., 2008; Michaelian et al., 2011).

Il existe diverses méthodes pour diminuer la vulnérabilité des forêts face aux changements climatiques. Cela passe par des pratiques sylvicoles, dites d'adaptation, visant à augmenter la résilience et/ou la résistance des forêts. Par exemple, les éclaircies sont largement mises en avant pour diminuer les conditions de stress hydrique attendues avec les changements climatiques. Elles ont des effets positifs sur la croissance des arbres aussi bien en condition normale de précipitations (McDowell et al., 2006) qu'en condition de sécheresse (Sohn et al., 2016a). Celles-ci permettent également de diminuer le taux de mortalité des arbres suite à des épisodes de sécheresse (Giuggiola et al., 2013).

Bien que les éclaircies apparaissent comme une pratique efficace pour diminuer le stress hydrique, leurs bénéfices ont majoritairement été documentés dans des conditions climatiques semi-arides (Simonin et al., 2007; del Campo et al., 2014). En effet, la réponse des forêts tempérées aux éclaircies n'a été que peu étudiée jusqu'à maintenant et les quelques études disponibles concernent des forêts tempérées européennes (Bréda et al., 1995). Par ailleurs, il existe peu de lignes directrices quant à la surface terrière résiduelle requise pour diminuer la compétition pour l'eau et ainsi retirer des bénéfices en période de sécheresse. En effet, la plupart des études comparent des peuplements avec et sans traitement d'éclaircie (Lagergren et al., 2008; Skubel et al., 2017) et très peu de recherches ont étudié différentes surfaces terrières résiduelles (Giuggiola et al., 2013; Bottero et al., 2017). Étudier la réponse des forêts tempérées du sud du Québec à un gradient de surface terrière résiduelle s'avère donc particulièrement pertinent afin de développer des pratiques sylvicoles adaptées aux conditions locales pour limiter les impacts des changements climatiques sur les forêts.

1.2 État des connaissances

1.2.1 Les conséquences des changements climatiques sur la disponibilité en eau

Voilà près d'une trentaine d'années que les effets des changements climatiques se font ressentir, générés par une augmentation des émissions de gaz à effet de serre. La température moyenne globale a augmenté de 0,85°C sur une période s'étalant de l'époque préindustrielle à nos jours (1850-2012, GIEC, 2014). Cette hausse entraîne une augmentation de la vapeur d'eau atmosphérique qui est un des facteurs d'accentuation des événements climatiques extrêmes tels que les vagues de chaleur, les ouragans et les fortes précipitations (Herring et al., 2014 ; Trenberth et al., 2015). Ainsi, une augmentation de la sévérité et de la durée des sécheresses est projetée à l'échelle globale (Dai, 2013) tout comme leur occurrence qui pourrait être multipliée par quatre d'ici 2100 (Cook et al., 2020). En effet, AP.Williams et al. (2020) ont démontré, par l'usage combiné de modélisation hydrologique et de dendrochronologie, que la période de 2000 à 2018 a été la plus sèche depuis la fin des années 1500 et la deuxième plus sèche depuis les 800 dernières années dans le sud-ouest des États-Unis. Cette méga-sécheresse a été attribuée au changement climatique induit par l'augmentation des gaz à effet de serre anthropogéniques.

Le Québec subit également une modification de son climat, avec une augmentation de 1 à 3 °C des températures annuelles moyennes entre 1950 et 2011 (Vincent et al., 2012). Les scénarios climatiques montrent que cette tendance ira en s'aggravant, d'ici 2050, une augmentation de 1,8 à 2,7 °C est projetée durant l'été (juin à août) et de 3 à 5 °C durant l'hiver (décembre à février, Logan et al., 2011). Jumelée à cette hausse des températures, une augmentation de la quantité annuelle des précipitations de l'ordre de 10 à 22 % est attendue dans le sud du Québec (Sillmann et al., 2013). Cette augmentation est principalement le produit d'une hausse des précipitations hivernales et printanières. Aucun consensus n'émerge entre les modèles climatiques globaux concernant les précipitations estivales, avec une projection à la hausse ou à la baisse selon les modèles (Donat et al., 2013). Toutefois, il est à prévoir que ces épisodes de précipitations estivaux seront plus intenses et moins bien répartis dans le temps. En effet, il est projeté que le sud du Québec sera touché par un plus grand nombre d'événements de précipitation extrême, avec par exemple, une augmentation du nombre de jours de pluie abondante (>10 mm) de 4 à 6 jours entre 1981-2000 et 2081-2100 pour la trajectoire d'émissions RCP8.5 (Sillmann et al., 2013).

Cette modification du climat aura probablement un impact sur la disponibilité en eau dans les écosystèmes forestiers du sud du Québec. En effet, une réduction de 15 % à 34 % de la disponibilité en eau dans le sol est projetée à l'horizon 2080 (Houle et al., 2012). Ainsi, une part importante de l'eau provenant des événements de précipitations extrêmes ne sera pas disponible pour la végétation du fait d'une perte importante de l'eau par drainage du sol (Figure 1.1). L'augmentation des températures et des conditions sèches pendant l'été favoriseront l'évapotranspiration via un allongement de la longueur de la période de croissance et une hausse de la demande évaporative de l'atmosphère (Audet et al., 2012).

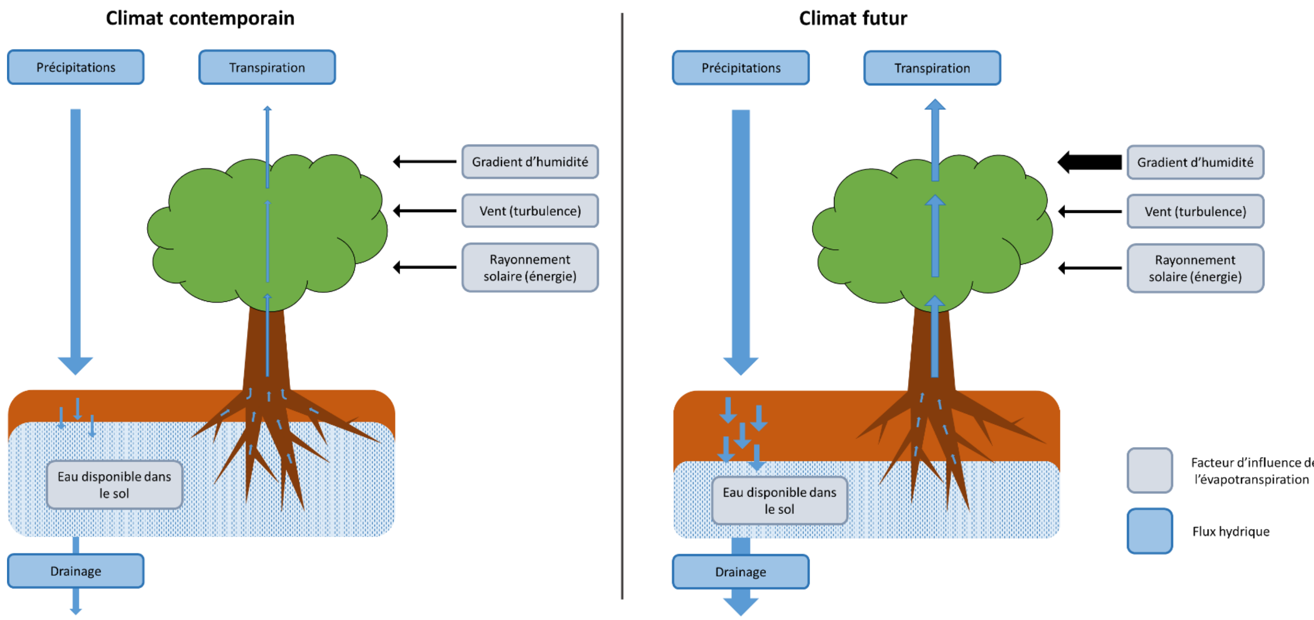

Figure 1.1 Représentation schématique de l'impact des changements climatiques sur les différents flux hydriques en milieu forestier

De plus, la demande évaporative de l'atmosphère est modifiée du fait d'une augmentation du déficit de tension de vapeur (Vapor Pressure Deficit ou VPD en anglais). Le VPD correspond à la différence entre la quantité de vapeur d'eau théorique que peut contenir l'atmosphère à saturation et la quantité réelle de vapeur d'eau présente dans l'atmosphère (Anderson, 1936). Une hausse des températures augmentera la quantité de vapeur d'eau théorique présente dans l'atmosphère à saturation menant à une augmentation du VPD. En réponse à cette hausse, les arbres verront leur taux de transpiration augmenter, dans la limite d'accès à une ressource en eau suffisante (Breshears et al., 2013). Ainsi, malgré la hausse des précipitations annuelles, la combinaison d'une augmentation des événements de précipitations extrêmes accroissant le drainage et d'une demande évaporative accrue de l'atmosphère risquent de réduire l'eau disponible pour les arbres dans les forêts tempérées québécoises.

1.2.2 Les sécheresses et leurs conséquences sur les forêts

Les sécheresses peuvent être définies comme « des événements climatiques récurrents durant lesquels les précipitations et l'eau disponible sont en dessous de leur seuil normal et qui peuvent toucher l'ensemble des régions du globe, même les plus humides » (Dai, 2011, traduction libre). Plusieurs types de sécheresse peuvent être distingués. La sécheresse dite météorologique correspond à une période où le déficit de précipitation est important. La sécheresse des sols correspond à des conditions d'humidité du sol largement sous la normale et venant impacter la zone racinaire des plantes. La sécheresse hydrologique, quant à elle, intervient après ces périodes et est caractérisée par des déficits dans le niveau des eaux de surface et souterraines (Van Loon, 2015).

Les sécheresses peuvent occasionner des événements de mortalité à grande échelle, dans les forêts tropicales, dans les forêts méditerranéennes, dans les forêts boréales, ou encore dans les forêts tempérées (Allen et al., 2010). En lien avec la sécheresse, une mortalité allant jusqu'à 90 % a été relevée chez *Pinus edulis* dans les forêts de l'ouest des États-Unis, à la suite de deux périodes de déficit hydrique du sol, respectivement de 10 et 15 mois, entre 2000 et 2003 (Breshears et al., 2005). Les forêts matures boréales canadiennes ont aussi subi une augmentation moyenne de 4.7 % de mortalité par an, indépendamment de l'espèce, sur une période s'étalant de 1963 à 2008 (C.Peng et al., 2011). Malgré les prédictions des potentiels bénéfices du réchauffement climatique à court terme sur la productivité des forêts boréales de l'ordre de 13 % (D'Orangeville et al., 2018a), des taux de mortalité anormaux ont pu aussi être enregistrés. Par exemple, dans les savanes boréales à peuplier faux-tremble (*Populus tremuloides*) de la Saskatchewan, une augmentation de près de 35 % de leur mortalité accompagnée d'une diminution de 30 % de leur croissance ont été observées à la suite d'importantes sécheresses ayant eu lieu sur une période de 12 mois entre 2001 et 2002 (Hogg et al., 2008; Michaelian et al., 2011). Des forêts tempérées sont aussi touchées, avec en France, une hausse annuelle de 1 % de la mortalité pour l'ensemble des espèces d'arbres qui a été enregistrée en 2004, faisant suite à l'importante sécheresse de l'été 2003 (Bréda et al., 2006). Dans les forêts tempérées du Québec, il a été montré que les effets négatifs de la sécheresse sur la croissance des arbres varient selon le mois de l'année. Les effets les plus importants sont observés lors de sécheresses ayant lieu au début de la saison de croissance (mai et juin) (D'Orangeville et al., 2018b).

Les sécheresses ont un impact négatif sur la physiologie des arbres. La répétition d'épisodes secs engendre des effets délétères sur les arbres que ce soit via des carences en carbone ou des défaillances hydriques (McDowell et al., 2008). Une faible disponibilité en eau dans le sol provoquera un stress hydrique qui aura pour conséquence d'augmenter la tension dans le xylème des arbres pouvant entraîner un phénomène de cavitation. Cela correspond à un remplacement de la phase liquide (sève brute) par une phase gazeuse (vapeur d'eau). Dans les cas d'une sécheresse prolongée ou sévère, la cavitation pourra entraîner une embolie du vaisseau conducteur. La vapeur d'eau sera remplacée par de l'air, insoluble avec la sève, rendant le vaisseau inefficace (Cruiziat et al., 2001). Une accumulation de conditions défavorables pourra accentuer ce phénomène et entraîner une augmentation de la sensibilité des arbres aux attaques d'insectes (Anderegg et al., 2015; Kolb et al. 2016) ou de pathogènes (Hogg et al., 2002; Weed et al., 2013).

1.2.3 Les pratiques pour l'adaptation des forêts

1.2.3.1 Concept théorique de la sylviculture d'adaptation

Pour contrer ces effets, diverses stratégies peuvent être mises en place pour permettre aux forêts de s'adapter aux nouvelles conditions climatiques propices à la création d'un stress hydrique. L'exploitation forestière peut avoir divers impacts sur la végétation de sous étage (Moola & Vasseur, 2008) ou encore sur les sols (Roy et al., 2021), cependant des pratiques sylvicoles dites d'adaptation se développent également afin d'aider les forêts à faire face aux changements climatiques (Millar et al., 2007; Millar et Stephenson, 2015; D'Amato et al., 2011). Une des démarches proposées se présente sous la forme d'un gradient d'action pouvant être réalisé dans les forêts et consistant à : ne pas intervenir, augmenter leur résistance, accroître leur résilience, promouvoir leur transition (Millar et al., 2007; Nagel et al., 2017).

Premièrement, la résistance d'une forêt est, par définition, sa capacité à absorber les perturbations et/ou les stress tout en maintenant des conditions inchangées (Holling, 1973). Les options pour l'augmenter peuvent être d'éliminer les espèces invasives ou encore de dégager les espaces à fort potentiel d'incendie (Millar et al., 2007). Pour répondre aux sécheresses tout en préservant une croissance acceptable, il est aussi envisageable d'effectuer des éclaircies de différentes intensités afin d'augmenter la disponibilité en eau et ainsi diminuer la compétition pour les ressources hydriques (Bottero et al., 2017). En effet, des arbres présents dans des parcelles fortement éclaircies présentent une meilleure croissance que ceux dans des parcelles moyennement et faiblement éclaircies (Bottero et al., 2017). Deuxièmement, la résilience quant à elle correspond à la capacité d'une forêt à recevoir une certaine quantité de perturbations tout en revenant à son état d'origine après celles-ci (Holling, 1973). La prise en compte des caractéristiques biotiques et abiotiques des milieux environnants (sol, climat, espèce animale ou végétale présente par exemple) peut être le premier pas pour accroître la résilience et la résistance d'un peuplement tout en adaptant les pratiques de gestions (Puettman et al., 2008). Troisièmement, les monocultures sont très sensibles aux changements climatiques et aux sécheresses et favoriser l'hétérogénéité en implantant de nouvelles espèces pour les rendre plus aptes à y répondre est aussi une autre option (Nagel et al., 2017). Ainsi, la transition consiste à prendre en considération les changements d'une forêt plutôt que d'y résister pour lui permettre d'avoir une réponse adaptée (Millar et al., 2007). Cette idée est abordée de manière similaire par KJ. Puettman qui incite les gestionnaires à « recréer la variabilité des perturbations naturelles, entre et dans les peuplements » (Puettman et al., 2008, traduction libre). Cela peut être abordé en conservant le patrimoine génétique du peuplement, ou en le modifiant, en introduisant de nouvelles espèces ou des individus d'une même espèce provenant d'autres populations (Grant et al., 2013). Des plantations dans des localisations différentes peuvent aussi permettre d'acclimater des espèces qui seront potentiellement adaptées à ce milieu dans un futur proche du fait des changements climatiques (*i.e.* accoutumer les espèces à une nouvelle aire de répartition géographique afin de réduire les stress liés au changement climatique) (Nagel et al., 2017). L'ensemble de ces propositions visent à développer une sylviculture plus durable dans le temps qui devra être combinée avec des pratiques de gestion déjà existantes.

1.2.3.2 L'apport des éclaircies sur la dynamique d'un peuplement forestier

Des pratiques sylvicoles telles que les éclaircies sont utilisées pour leur effet bénéfique sur la croissance et la survie des arbres face à des conditions plus sèches. Cette pratique sylvicole est largement mise en avant pour préserver la productivité des forêts face aux sécheresses (Grant et al., 2013). Quelques études ont évalué l'effet de l'éclaircie sur le développement des arbres en forêt tempérée en régime de précipitation normal car celle-ci a pour effet d'accroître la disponibilité en eau dans le sol via une réduction de l'évapotranspiration journalière (Aussenac et Granier, 1988; Bréda et al., 1995). Le bénéfice qui en découle est une croissance accrue des arbres tant dans des peuplements de conifères que de feuillus (Aussenac et Granier, 1988; Bréda et al., 1995; McDowell et al., 2006). Le statut social de chaque arbre peut aussi être pris en compte lors d'une éclaircie, en tenant compte que les arbres dominants et co-dominants de la strate supérieure du peuplement ont accès à plus de ressources (énergie solaire, eau) que les arbres de la strate inférieure. En effet, une éclaircie de la strate inférieure aura plus de bénéfices qu'une éclaircie de la strate supérieure sur le taux de mortalité (Powers et al., 2010). Cela montre que des traitements réguliers sur la strate inférieure pourraient avoir un effet bénéfique sur la résistance de l'ensemble du peuplement. En somme, les éclaircies permettent de réduire la surface terrière des peuplements, diminuant la compétition pour les ressources et de ce fait la mortalité.

Outre les bénéfices des éclaircies sous des conditions normales, les effets des éclaircies peuvent aussi être évalués dans un contexte de sécheresse, lorsque les ressources hydriques disponibles sont largement sous la normale. Il a été montré qu'une éclaircie modérée à importante, a des effets bénéfiques sur la résistance et la résilience, avec de meilleurs taux de croissance des peuplements pendant et après des épisodes de sécheresse (Sohn et al., 2016a; Bottero et al., 2017; Giuggiola et al., 2013; D'Amato et al., 2013). Ces résultats peuvent s'expliquer par le fait que la densité relative d'un peuplement est corrélée négativement avec la résistance et la résilience à la sécheresse, c'est-à-dire qu'un peuplement grandissant à faible densité (éclaircie importante) sera moins vulnérable à la sécheresse (Bottero et al., 2017). La taille des arbres des peuplements joue aussi un rôle : un peuplement âgé avec des arbres plus grands serait moins résistant et moins résilient pour répondre à des épisodes de sécheresse. En effet, il a été démontré que les éclaircies permettaient de compenser le déclin de la résistance au stress hydrique d'une population d'arbres âgés (D'Amato et al., 2013; Sohn et al., 2016b). Les éclaircies apparaissent donc comme un bon moyen pour assurer la viabilité des peuplements en atténuant les effets des épisodes de sécheresse. Néanmoins, l'ensemble de ces résultats peuvent être nuancés. En effet, des études ont montré que les bénéfices dans le temps des éclaircies sont corrélés négativement avec le taux de croissance et la résilience des peuplements quand intervient un épisode de sécheresse (Sohn et al., 2016a; Sohn et al., 2016b). Cela signifie que, plus la période depuis la dernière éclaircie est longue, moins l'avantage qu'elle procure sur le maintien du taux de croissance et sur la résilience sera décelable suite à un épisode de sécheresse.

Pour terminer, si l’on s’intéresse à l’ensemble de ces études, certains points peuvent être mis en exergue. Une grande majorité des études se déroulent en climat aride ou méditerranéen et se concentrent principalement sur des espèces de conifères. Sohn *et al.*(2016a) ont recensé 23 études parmi lesquelles 17 ont étudié la réponse de conifères aux éclaircies contre seulement six pour des espèces feuillues, et aucune n’impliquant de peuplements feuillus en Amérique du Nord. Avec ces observations, il semble pertinent qu’une étude soit menée dans des peuplements de feuillus en forêt tempérée nord-américaine afin d’adapter les traitements d’éclaircie à de futurs épisodes de sécheresse.

1.3 Objectifs et hypothèses de travail

L’objectif principal de cette étude était de déterminer comment un gradient de surface terrière résiduelle, créé après traitements d’éclaircie, affecte la transpiration d’arbres feuillus en forêt tempérée. L’érable rouge (*Acer rubrum*, L), une espèce d’arbre feuillue largement distribuée en Amérique du Nord (Burns & Honkala, 1990), a été sélectionné afin d’observer sa réponse à des éclaircies de différentes intensités. Nos objectifs spécifiques étaient de décrire comment différentes surface terrière résiduelles influencent i) les conditions microclimatiques, ii) la densité de flux de sève à l’échelle de l’arbre et iii) la transpiration du peuplement. Nous avons fait l’hypothèse que la compétition pour la ressource hydrique augmente avec la surface terrière résiduelle entrainant un Fd plus faible dans les parcelles avec une grande surface terrière résiduelle et un Fd plus important dans les parcelles avec une faible surface terrière résiduelle.

CHAPITRE II

SHORT-TERM EFFECT OF THINNING ON RED MAPLE TRANSPIRATION IN A MIXED TEMPERATE FOREST

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2.1 Abstract

Under climate change, forests are expected to experience drier conditions that may increase tree mortality. Silvicultural treatments such as thinning have been used to reduce competition for water resources and improve forest resistance to drought events. Most studies have investigated the effectiveness of thinning treatments in semi-arid conditions and little information is available regarding the response of temperate forests as well as the residual basal area required to rip benefits of these treatments. This research aims to understand how different residual basal area influence transpiration in mixed forest stands dominated by red maple (*Acer rubrum*) in southeastern Canada. We monitored sap flux density (Fd) with thermal dissipation type sensors for 18 red maple trees spread across nine experimental plots thinned to obtain a gradient of residual basal area (20, 12.5, 6 m^2 ha^{-1}). During the first growing season following treatments, low residual basal area (6 m^2 ha^{-1}) induced drier atmospheric conditions as shown by a significantly greater vapor pressure deficit (VPD) compared to high residual basal area plots (20 m^2 ha^{-1}). At the tree scale, Fd increased with residual basal area, with the most pronounced differences under dry atmospheric conditions: when daily VPD exceeded 1.1 kPa, mean Fd in high residual basal area plots was respectively 20 % and 75 % greater than in medium (12.5 m^2 ha^{-1}) and low residual basal area plots. Still, we found considerable variability at the site-level regarding the response of Fd to residual basal area treatments. At the stand level, we simulated total transpiration for stands made up of only red maples and transpiration in medium and low residual basal area plots amounted to 41 % and 79 % of the transpiration simulated for the high residual basal area plot. Overall, this work highlighted the large variability of temperate forests in response to residual basal area treatments, emphasizing the need to better model the water budget of forests and the partitioning of overstory and understory evapotranspiration to make adequate residual basal area prescriptions in temperate forests.

Keywords: sap flux density, residual basal area, transpiration, red maple, vapor pressure deficit, hydrology

2.2 Introduction

Climate change has led to an increase in global mean temperature of 0.85 °C for the 1850–2012 period (IPCC, 2014). At the global scale, it is projected that climate change will lead to an increase in drought severity and duration (Dai, 2013). Recent research showed that droughts, including extreme events, will be 50 % more frequent (2071-2100) in southern Europe compared to actual conditions (1981-2010) under RCP 8.5 (Spinoni et al., 2018). In southeastern Canada, temperature have increased by 1 to 3 °C between 1950 and 2011 (Vincent et al., 2012), and will continue to rise by 2050 with a projected increase of 1.8 to 2.7 °C during summer (June to August) and 3 to 5 °C during winter (December to February, Logan et al., 2011). These warming air temperatures translate into an increase in the atmospheric moisture demand, an important driver of drought-induced tree mortality (Grossiord et al., 2020). Indeed, a rise in vapor pressure deficit (VPD) can increase soil evaporation and tree transpiration thus reducing soil water availability (Breshears et al., 2013). In addition to widespread atmospheric drying, more extreme precipitations events are expected in southeastern Canada and annual precipitations are expected to slightly increase or remain stable (Sillmann et al., 2013). These changes in the precipitation regime may lead to an increased deep drainage and longer period between precipitations events that may aggravate soil water stress in temperate ecosystems (Knapp et al., 2008). In forest of southeastern Canada, growing-season soil water availability is overall projected to decreased by 15 % to 34 % by the 2080 horizon compared to contemporary conditions (Houle et al., 2012).

Reduced water availability can reduce tree growth (Ruehr et al., 2015) or in extreme cases, cause tree death, through hydraulic failure due to repeated cavitation (McDowell et al., 2008; Hartmann et al., 2018). Drought-induced mortality of trees has been observed in numerous forests around the world (Allen et al., 2010). For example, across Europe, forest mortality exceeding long-term mortality levels was significantly related to the monthly water balance (Senf et al., 2020). Mesic temperate forests where precipitations are typically abundant are vulnerable to droughts. For example, drought has been found to be similarly detrimental to tree growth at wet, mesic and xeric sites across the temperate forests of western Caucasus (Martin-Benito et al., 2018). In the Ozark Highlands forest (USA), red oak trees experienced an increased mortality rate from 6-8 % in 1999 to 15 % in 2010 following drought events (Fan et al., 2012). In the Morgan-Monroe State forest (USA), soil water stress induced a tree growth reduction of 15-20 % over the 1999-2011 period (Brzostek et al., 2014). In eastern North-America, the reduction of tree growth was also more pronounced when droughts occurred at the beginning of the growing season (D'Orangeville et al., 2018a).

Silvicultural practices can be established to mitigate the impact of droughts. In recent years, water oriented forest management was recommended including thinning, irrigating or selecting species adapted to drier conditions (Grant et al., 2013; Field et al., 2020). Devising strategies to face water stress is a long process that needs to be tested from a theoretical framework to a practical framework (Gustafson et al., 2020). Thinning is a well-known practice to reduce competition for water resources and attenuate the detrimental impact of droughts on tree growth (Bréda et al., 1995; Manrique-Alba et al., 2020). However, the beneficial effect of this practice varies according to the treatment intensity. Indeed, trees in high thinning intensity stands (residual basal area ≤ 14 m^2 ha^{-1}) maintained a greater growth rate compared to medium (residual basal area = 23 m^2 ha^{-1}) and low thinning intensity stands (residual basal area ≥ 28 m^2 ha^{-1}) (Bottero et al., 2017). Still, little guidance is offered regarding the level of thinning intensity or the optimal residual basal area required to reduce water stress in temperate mixed forests. Indeed, thinning prescriptions in temperate forests need to balance the benefits associated with a reduction in stand density during droughts with potentially marginal benefits during more typical growing seasons with ample precipitations. Moreover, studies on the benefits of thinning have mainly been conducted under semi-arid conditions (Simonin et al., 2007; del Campo et al., 2014), with only few studies available in temperate forests (Bréda et al., 1995; D'Amato et al., 2013). The majority of studies on the reduction of water stress through thinning have also focused on coniferous tree species with little information available on deciduous tree species. Indeed, a meta-analysis of 23 studies looking at the reduction of water stress through thinning listed 17 studies on coniferous tree species (Sohn et al., 2016). Only one study looked at a deciduous species in a temperate forest and it was located in Europe (Bréda et al., 1995).

Under our changing climate, it appears relevant to understand the response of red maple (*Acer rubrum*, L.), an abundant deciduous tree species with a widespread repartition in North America (Burns & Honkala, 1990), to different thinning treatments. The main objective of this research was to assess how a gradient of residual basal area (BA) influenced tree transpiration in a mixed temperate forest. Our specific objectives were to describe how different residual BA treatments influence i) microclimatic conditions, ii) tree-scale sap flux density (Fd) and iii) stand-scale transpiration. We hypothesized that competition for water resources increases with residual BA which will lead to smaller Fd in plots with high residual BA and greater Fd in plots with low residual BA.

2.3 Materials and methods

2.3.1 Site description

The study was conducted in a mixed temperate forest in southern Quebec, Canada (45.98°, 72.62°). The study area is located in the Saint Lawrence Lowlands and soils correspond to the Saint-Amable sand complex along with the Saint-Sylvère sandy loam or sandy rocky loam (Choinière, 1960). At the study sites, red maple (*Acer rubrum*, L.) is the dominant tree species. We studied red maple, a diffuse porous species, for its inherent characteristics. Indeed, red maple is considered to be one of the least sensitive tree species to drought (Boisvert-Marsh et al., 2020) because of its good adaptive capacity to climate change (Royer-Tardif et al., 2021). Its distribution area is projected to be modified by 11 % to 15 % by 2040 due to an increased exposure to drought (Aubin et al., 2018), which made red maple an important species to study in a changing climate context. In addition, trembling aspen (*Populus tremuloides*, Michx.), white pine (*Pinus strobus*, L.), balsam fir (*Abies balsamea*, (L.) Mill.), jack pine (*Pinus banksiana*, Lamb.) and paper birch (*Betula papyrifera*, Marsh.) co-occurred at different densities at the study sites. At the nearest weather station (station 7022160, 14 km from study site), mean annual temperature is 6.4 °C and mean annual precipitation is 1113 mm for the 1981-2010 period (Environment Canada, 2020).

2.3.2 Thinning treatment

The experimental design used for this study is part of an experiment aiming at testing different silviculture of adaptation strategies in red maple mixed stands (Thiffault et al., 2021). The design consisted of three sites, each subdivided into three adjacent 50 m x 50 m plots. Site 1 was located 0.6 km away from site 2 and 4 km away from site 3. At each plot, trees with a diameter at breast height (DBH) greater than 9 cm were surveyed during the summer 2019. Pre-treatment BA of the nine plots, varied between 19.1 m^2 ha^{-1} and 45 m^2 ha^{-1} (Table 2.1). In the following winter (2019-2020), thinning was performed in adjacent plots to obtain high residual BA (20 m^2 ha^{-1}), medium residual BA (12.5 m^2 ha^{-1}) and low residual BA (6 m^2 ha^{-1}). Thinning treatments were performed at all sites except at site 2 where one plot with an initial BA of 19.1 m^2 ha^{-1} did not receive any treatment and was considered as a plot with a high residual BA. Small variation in post-treatment residual BA are explained by the margin of error (± 0.5 m^2 ha^{-1}) of operations which may result in slight difference between sites, like in the high and low residual BA plots of site 1 (Table 2.1). Tree removal was performed to prioritize trees of poor health status and to evenly distribute the remaining standing trees across the plot.

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Table 2.1 Plot characteristics before and after thinning treatments, including basal area (BA), percentage of basal area made up of red maple, other deciduous trees, coniferous trees and effective leaf area index (LAI)

		Site 1			Site 2			Site 3		
	Residual BA treatment	High	Medium	Low	High	Medium	Low	High	Medium	Low
Initial (before thinning)	BA (m^2 ha^{-1})	28.0	32.7	27.1	19.1	19.2	21.4	24.4	40.3	45.0
	% BA: red maple	62	62.0	57	88	65	63	80	56	38
	% BA: other deciduous trees	12	12	3	6	12	24	20	42	62
	% BA: coniferous trees	26	26	40	6	23	13	0	2	0
Residual (after thinning)	BA (m^2 ha^{-1})	20.1	12.5	6.5	19.1	12.5	6.0	20.0	12.5	6.0
	% BA removal	27	62	76	0	35	72	18	69	87
	effective LAI (m^2 m^{-2})	2.1	1.1	0.7	2.9	1.3	0.9	2.4	1.4	0.9
	% BA: red maple	56	81	77	88	80	75	93	58	50
	% BA: other deciduous trees	13	0	1	6	2	4	7	42	50
	% BA: coniferous trees	31	19	22	6	18	21	0	0	0

2.3.3 Sap flow measurements

From June 17th to August 31st, 2020 (*i.e.* the summer following thinning treatments), we used 20 mm-long heat dissipation sensors to measure xylem Fd (cm h^{-1}) on red maple. Within each plot, we selected two vigorous and healthy red maples according to two classes of DBH, *i.e.* a small size class with DBH ranging between 9 cm and 18 cm and a large size class with DBH greater than 23 cm (n_{trees} = 18). The DBH of selected trees varied between 13 cm and 17.5 cm for trees in the small size class while it varied between 24 cm and 52 cm for trees in the large size class. We inserted sensors at a depth of 0-20 mm beneath the cambium for trees in the small size class while we inserted two sensors per tree, at depths of 0-20 mm (outer position) and 20-40 mm (inner position) for trees in the large size class in order to capture the radial variation of Fd. Indeed, it is known that Fd is not uniformly distributed along sapwood (Lu et al., 2004).

Heat dissipation sensors were self-manufactured and followed Granier's design (Granier, 1985). Before their installation, we removed tree bark to provide a direct contact between the sensors and the sapwood. Each sensor was inserted on the north side of the tree at a height of 1.35 m and protected with thermal insulation to avoid direct solar incidence (Lu et al., 2004). The upper and lower probes were aligned vertically, 10 cm apart. The upper probe was heated with a lead-acid battery supplying a constant current of 0.2 V while the lower probe was unheated. We coated probes with thermal grease and inserted them in aluminum tubes to ensure an even repartition of the heat. The temperature difference between the two probes (ΔT) was measured with a copper-constantan thermocouple placed in each of them. ΔT was recorded every 30s and averaged to a 15-minutes time step which was stored in a data logger (Arduino Uno). Recorded ΔT (°C) were converted into Fd (cm s^{-1}) based on the empirical equation derived by Granier (Granier, 1987):

$$F_d = 0.0119 * K^{1,231} \tag{1}$$

in which K is the dimensionless index of sap flux:

$$K = (\Delta T_{max} - \Delta T)/\Delta T \tag{2}$$

where ΔT_{max} (°C) is the temperature difference between the two probes under zero flux conditions at nighttime. Using the *Aquaflux* R package, v0.5-1 (Speckman et al., 2020), ΔT_{max} was computed for each sensor at multiple time points that satisfied the following criteria: i) corresponds to the local maximum, ii) occurs at night and iii) occurs when VPD ≤ 0.2 kPa for at least two hours. Giving gaps in data, ΔT_{max} were manually selected following these criteria and linearly interpolated to provide a baseline to compute Fd values for the entire time series. Hourly VPD was calculated following Murray (1967), using air temperature and relative humidity measurements performed at each plot with LogTag sensors (Haxo-8, ± 0.5 °C and ± 3 %). Sensors were positioned at a height of 2 m on a nearby tree and were covered with a plastic shield to avoid direct solar incidence. To obtain daily VPD, we averaged hourly VPD values over the entire day (00:00 to 23:00).

For red maple in the small size class, whole-tree sap flow was computed by upscaling Fd to the tree sapwood area. The sapwood area of each trees (A_{s_tree}, cm^2) was estimated using the allometric equation for red maple derived by Wullschleger in Tennessee, USA (Wullschleger et al., 1998):

$$A_{s\_tree} = B0 * DBH^{B1}$$
(3)

where DBH (cm) is the diameter at 1.3 m height and B_0 and B_1 are empirical coefficients (B_0 = 0.638 and B_1 = 1.986).

For red maples in the large size class, we first tested for the presence of radial variation (see section 2.3.5). In light of results, we considered it when computing whole-tree sap flow:

$$Q_{tree} = \sum_{z=1}^{s} F_{d,z}\, A_{s\_tree,z} \tag{4}$$

where Q_{tree} ($cm^3\ s^{-1}$) is the whole-tree sap flow, $F_{d,z}$ is the sap flux density measured at depth *z* (z = 0-20 mm, 20-40 mm), $A_{s\_tree,z}$ (cm^2) is the tree sapwood area of concentric annuli at depth *z*. To obtain daily sap flow, we integrated hourly sap flow values over daytime (6:00 to 22:00).

To assess how Fd values measured at the tree scale translate into total transpiration at the stand scale, we simulated transpiration of stands made up solely of red maples with residual BA 20, 12.5, 6.5 $m^2\ ha^{-1}$. Stand transpiration was computed as:

$$E_t = \frac{\sum_{i=1}^{n} Q_{tree,i}}{A_G} \tag{5}$$

where E_t is the stand transpiration rate ($cm\ s^{-1}$), $Q_{tree,i}$ ($cm^3\ s^{-1}$) is the daily whole-tree sap flow of tree *i*, *n* is the number of trees in the plot and A_G is the plot ground area (cm^2). We computed Q_{tree} by using Fd values and tree sizes (DHP) inventoried at site 1. We chose this site to avoid extreme Fd values associated with the two other sites (see *Results* below). We gap-filled days with missing Fd values to allow the comparison of transpiration between plots. To do so, we used linear regression equations based on linear models with Fd as the response variable and VPD as the explanatory variable. Gap-filled Fd values were only used to simulate stand transpiration and were not used in statistical analyses (section 2.3.5). E_t was integrated over time to obtain total stand transpiration (mm) over the study period (76 days from June 17th and August 31st, 2020).

2.3.4 Leaf area index measurements

We measured the leaf area index (LAI) with a LAI-2000 plant canopy analyzer (Li-Cor Biotechnology) in September 2020 (leaf-on). We simultaneously measured below the canopy and in an adjacent open field using two devices. Measurements were performed at a height of 1.5 m above the ground. Below canopy measurements were made along four transects (N to S, E to W, NE to SO and NO to SE). Measurements were recorded every 15 seconds at one-meter interval along transects, during 15 minutes for a total of 60 readings per plot. To avoid direct solar radiation, measurements were performed under diffuse light conditions at dawn or dusk. The effective LAI was computed with the FV2000 software. Below-canopy and open-field measurements were matched by time and a random distribution of foliage was assumed.

2.3.5 Statistical analysis

Fd and VPD values were averaged to daily values after checking for gaps in our data. We excluded days from the analysis if they had gaps in data of more than four hours. We also excluded days where atmospheric humidity is close to saturation (daily VPD < 0.2 kPa) as daily Fd was low on these days (values smaller than 3.65 cm h^{-1}). In total, our analysis focused on daily time series comprising 49, 43 and 48 days for site 1, 2 and 3, respectively, over our 76 days long study period. Using the *glmmTMB* package (Brooks et al., 2017), we fitted three generalized linear mixed models (GLMM) to test the effect of residual BA on daily VPD and Fd as well as the presence of radial variation on daily Fd.

To assess the effect of residual BA on VPD, we used a GLMM with a Gamma distribution (link = log). To model daily VPD (n = 9 microclimatic sensors), we set the residual BA (categorical variable; low, medium and high residual BA) as a fixed covariate. We set a random intercept, that is the plot variable nested within the site variable and crossed with the day of the year, to address the lack of independence between plots within the same site. We did not include a random slope due to convergence issue.

To assess the effect of residual BA on Fd, we fitted a GLMM with a Gamma distribution (link = log). To model daily Fd at 0-20 mm depth (*n* = 18 trees), we set the residual BA and ln-transformed VPD (continuous variable) as fixed covariates. We also included the interaction between residual BA and ln-transformed VPD. VPD was included as a covariate to control for microclimatic differences between residual BA treatments and given that it has been shown to be a strong predictor of daily Fd (Oogathoo et al., 2020). We set a random intercept, that is the tree variable nested within the site variable and crossed with the day of the year, to address the lack of independence between trees within the same site. We specified ln-transformed VPD as a random slope because its relationship with Fd may have differed depending of the residual BA applied to the plot. We included a first order autoregressive covariance structure to take into account the repeated measures over time. In exploratory analyses, we ran the model without a random slope and with additional covariates (tree DBH, plot LAI, plot initial BA, Δ BA that is the difference in plot BA before and after thinning treatment and daily precipitation, Table S1). We chose not to include these variables to keep the most parsimonious model as AIC gains were minimal (maximum ΔAIC = 14).

To assess the presence of radial variation in Fd, we used a GLMM with Gamma distribution (link = log). To model daily Fd (*n* = 18 sensors), we set sensor position (categorical variable; outer for 0-20 mm insertion and inner for 20-40 mm insertion) and ln-transformed VPD as fixed covariates. We also included the interaction between sensor position and ln-transformed VPD. We set a random intercept, that is the sensor variable nested within the tree variable and crossed with the day of the year, to address the lack of independence between sensors within the same tree. We did not include a random slope due to convergence issue but we included a first order autoregressive covariance structure to take into account the repeated measures over time.

We validated model assumptions by plotting Pearson residuals against fitted value and against explanatory variables (Zuur & Ieno, 2016). A second step of validation was made with the *DHARMa* package (Hartig, 2021). A quantile-quantile plot of model residuals was made to test the normality of random effects. (Harrison et al., 2018). We also assessed residuals for temporal independence by looking at residual autocorrelation for each trees and sensors. We checked for multicollinearity of covariates by computing variation inflation factors with the *car* package (Fox & Weisberg, 2019). All analyses were performed with the R software (R Core Team, 2019).

2.4 Results

2.4.1 Meteorological conditions

Summer 2020 was characterized by a warm and dry late spring and early summer, followed by a wet late summer period. In June, mean air temperature (19.7 °C) was above the 1981–2010 normal (18.4 °C) while precipitations (59.1 mm) were almost half of normal levels (102.3 mm). The monthly Standardized Precipitation-Evaporation Index (SPEI) was equal to -1.80 (retrieved from the online SPEI Global Drought Monitor, Vicente-Serrano et al., 2010), which is below the -1.5 threshold, indicating a potential drought event with an important water availability deficit (D’Orangeville et al., 2018b). July was warm with mean air temperature (23.1 °C) above the climate normal (20.9 °C) while precipitations (89.7 mm) were close to the normal (106.2 mm), with the monthly SPEI slightly below equilibrium (-0.52). Mean August temperature (19.9 °C) was close to the normal (19.7 °C) while precipitations (181.7 mm) were nearly twice as much as the normal (106 mm). Accordingly, the monthly SPEI (+1.24) indicated an above average water availability.

2.4.2 Plot composition before and after treatment

The initial BA before treatment, varied between 45 m^2 ha^{-1} and 19.1 m^2 ha^{-1} (Table 2.1). High, medium and low residual BA were pre-established at 20, 12.5 and 6 m^2 ha^{-1} which lead to important variation in BA reduction. For example, the medium residual BA treatment resulted in a 62 %, 35 % and 69 % BA reduction at site 1, 2 and 3, respectively. Residual LAI decreased with the residual BA. The LAI of high residual BA plots (20 m^2 ha^{-1}) was approximately two and three times greater compared to medium (12.5 m^2 ha^{-1}) and low (6 m^2 ha^{-1}) residual BA plots.

Overall, red maple was the dominant species at all plots, except in the low residual BA plot of site 3. Initial composition at site 1 and 2 was typical for a temperate mixed forest with at least 60% of deciduous trees and less than 40% of coniferous trees per plots (Table 2.1). Red maple trees co-occurred with paper birch (*Betula papyrifera*, Marsh.), quaking aspen (*Populus tremuloides*, Michx.), white pine (*Pinus strobus*, L) and eastern hemlock (*Tsuga canadensis*, L.). Composition at site 3 was dominated by red maples and big tooth aspens *(Populus grandidentata*, Michx). After treatment, red maple represented at least 50 % of the residual BA in each plots, varying between 50 % and 93 %.

2.4.3 Influence of residual basal area on microclimatic conditions

In high residual BA plots, VPD was significantly lower than in low residual BA plot (Table 2.2). For example, at sites 2 and 3, mean VPD in high residual BA plots was respectively 25 % and 20 % lower than in low residual BA plots (Figure 2.1). These differences can be tied back to cooler temperatures associated with high residual BA plots as relative humidity remained similar between residual BA treatment. At sites 2 and 3, mean temperatures in high residual BA plots were respectively 1.4 °C and 1.1 °C lower than in low residual BA plots, whereas at site 1, the difference was close to 0.6 °C. In contrast, the differences in mean relative humidity between high and low residual BA plots did not exceed 1 % at any sites. Moreover, there was no significant differences in VPD between medium and high residual BA plots, or between medium and low residual BA plots (Table 2.2). The effect of medium residual BA on the atmospheric water demand varied largely from site to site (Figure 2.1). At site 1, mean VPD was similar among plots with no discernable effect of residual BA. At site 2, mean VPD of the medium residual BA plot was lower than the low residual BA plot but similar to the high residual BA plot, while it was the opposite at site 3 with low and medium residual BA plots exhibiting greater VPD than the high residual BA plot.

Table 2.2 Generalized mixed model describing daily vapor pressure deficit (VPD, kPa) as a function of residual basal area (BA) gradient, including high residual basal area (20 m^2 ha^{-1}), medium residual basal area (12.5 m^2 ha^{-1}) and low residual basal area (6 m^2 ha^{-1}).

Reference		Estimate	Standard error	*z* value	*p*-value
High residual BA	intercept	-0.54	0.09	-5.88	< **0.01**
	Medium residual BA	0.15	0.10	1.56	0.12
	Low residual BA	0.28	0.10	2.86	< **0.01**
Low residual BA	intercept	-0.27	0.09	-2.90	< **0.01**
	High residual BA	-0.28	0.10	-2.86	< **0.01**
	Medium residual BA	-0.13	0.10	-1.30	0.19

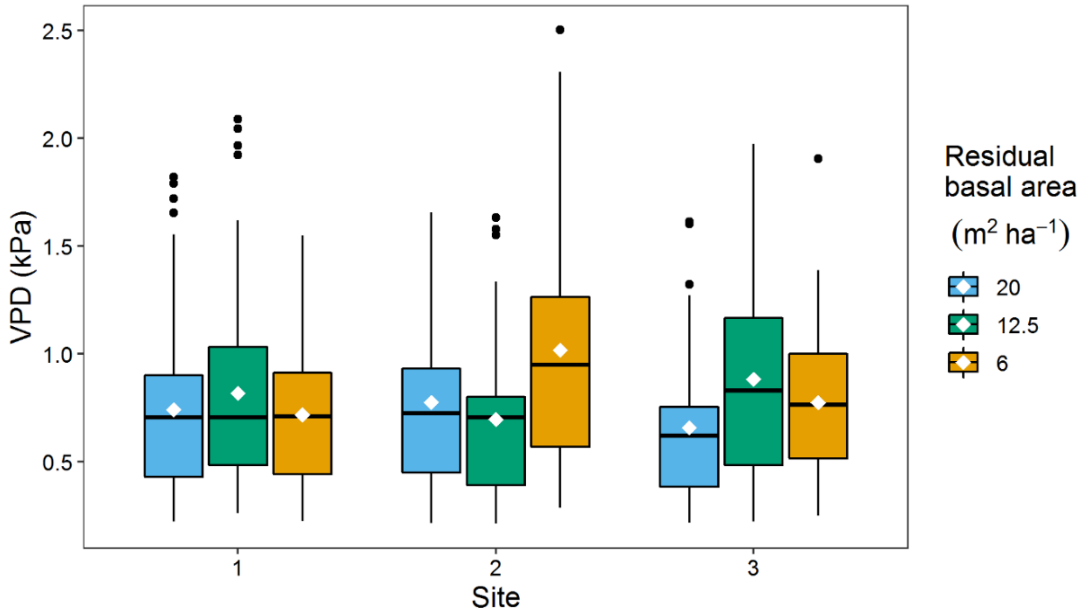

Figure 2.1 Mean daily vapor pressure deficit (VPD, kPa) at the three study sites. Each boxplot corresponds to an experimental plot with high residual basal area (20 m^2 ha^{-1}), medium residual basal area (12.5 m^2 ha^{-1}) or low residual basal area (6 m^2 ha^{-1}). Diamonds correspond to the mean, central lines are the median, whiskers represent lower or upper values observed within 1.5 times the interquartile range, and black points are outliers.

2.4.4 Influence of residual basal area on sap flux density

Mean Fd was greater in high residual BA plots than in low residual BA plots regardless of the VPD conditions, as shown by the significant main effect of the low residual BA (Table 2.3). Furthermore, Fd in high residual BA plots was significantly greater than both medium and low residual BA plots, although this effect varied according to VPD conditions as shown by the significant interaction between the ln-transformed VPD and residual BA (Table 2.3). Indeed, Fd differences between residual BA treatments were most pronounced during days with high VPD (≥ 0.8 kPa, Figure 2.2). For example, when daily VPD ranged between 0.8 and 1.1 kPa, mean Fd in the high residual BA plots was respectively 10 % and 30 % larger compared to the medium and low residual BA plots. We observed the most pronounced differences in Fd between different residual BA when daily VPD exceeded 1.1 kPa. Mean Fd for the high residual BA plot was respectively 20 % and 75 % greater compared to the medium and the low residual BA plots. In addition, in high residual BA plots, mean Fd increased with VPD, with almost a two-fold increase in the 0.2 to 0.4 kPa class (mean = 5.6 cm h^{-1}) compared to the > 1.1 kPa class (mean = 10.2 cm h^{-1}, Figure 2.2). In contrast, mean Fd varied little between VPD classes for low residual BA plots, with values ranging between 4.8 cm h^{-1} and 6.2 cm h^{-1}.

Figure 2.3 shows the plot-level relationship between Fd and VPD for the three residual BA treatments. While the tree nested within the site were defined as a random effect in the GLMM (Table 2.2), we showed plot-level relationships in Figure 2.3 to illustrate how the effect of the residual BA varied from site to site. At site 3, the high residual BA plot had Fd values that exceeded those in the medium and low residual BA plots. This is especially the case under conditions of large atmospheric demand when VPD reached values between 0.8 kPa (ln(VPD) = -0.2) and 1.6 kPa (ln(VPD) = 0.47). Indeed, daily Fd at the high residual BA plot ranged, between 8 cm h^{-1} and 21 cm h^{-1} compared to daily Fd that remained under 7 cm h^{-1} at the medium and low residual BA plots (Figure 2.3c). We observed a similar pattern, but to a lesser extent at site 1. The high residual BA plot had Fd values that exceeded those in the medium and low residual BA plots when VPD exceeded 0.8 kPa (ln(VPD) = -0.2). Daily Fd varied between 7.5 and 13.5 cm h^{-1} at the high residual BA plot while daily Fd remained below 10 cm h^{-1} at the medium and low residual BA plots (Figure 2.3a). Site 2 showed a different pattern than the two other sites, with the largest daily Fd values, generally ranging between 9 and 25 cm h^{-1}, in the medium residual BA plot (Figure 2.3b). In comparison, daily Fd remained below 10 cm h^{-1} at low and high residual BA plots at site 2.

Table 2.3 Generalized mixed model describing daily sap flux density (Fd, cm h^{-1}) as a function of residual basal area (BA) gradient, including high residual basal area (20 m^2 ha^{-1}), medium residual basal area (12.5 m^2 ha^{-1}) and low residual basal area (6 m^2 ha^{-1}).

Reference		Estimate	Standard error	*z* value	*p*-value
High residual BA	intercept	2.11	0.14	14.70	< **0.01**
	ln(VPD)	0.43	0.08	5.72	< **0.01**
	Medium residual BA	-0.05	0.20	-0.24	0.81
	Low residual BA	-0.40	0.20	-1.99	< **0.05**
	ln(VPD) : Medium residual BA	-0.17	0.08	-2.15	< **0.05**
	ln(VPD): Low residual BA	-0.30	0.08	-3.69	< **0.01**
Low residual BA	intercept	1.72	0.14	11.99	< **0.01**
	ln(VPD)	0.13	0.07	1.73	0.08
	High residual BA	0.39	0.20	1.99	< **0.05**
	Medium residual BA	0.35	0.20	1.75	0.08
	ln(VPD) : High residual BA	0.30	0.08	3.69	< **0.01**
	ln(VPD): Medium residual BA	0.13	0.08	1.56	0.12

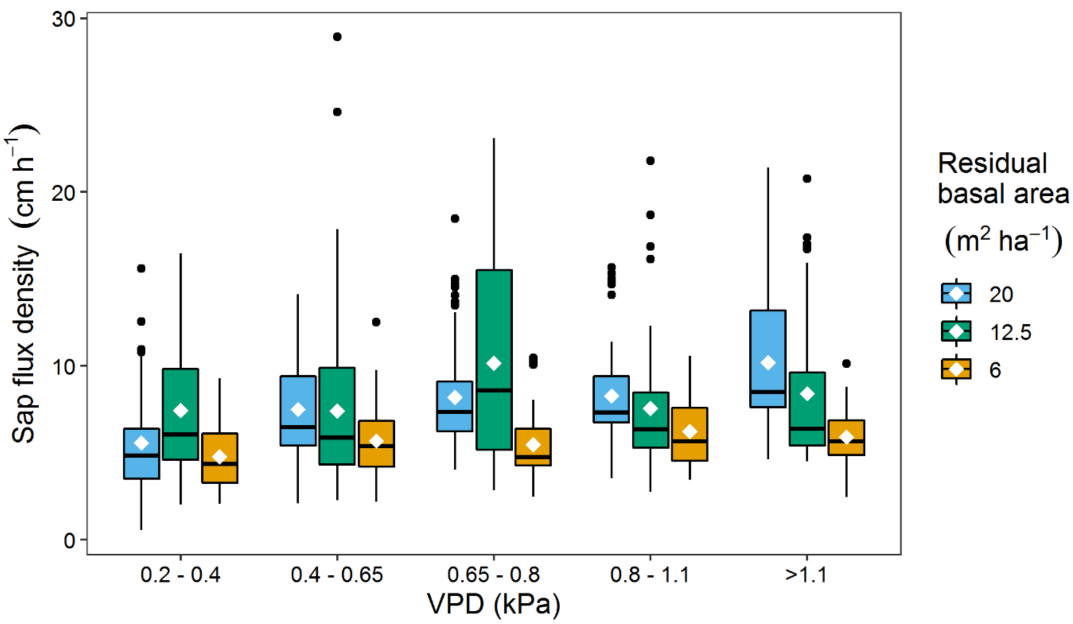

Figure 2.2 Daily sap flux density (Fd, cm h^{-1}) as a function of daily vapor pressure deficit (VPD, kPa) for a gradient of residual basal area treatments, including high residual basal area (20 m^2 ha^{-1}), medium residual basal area (12.5 m^2 ha^{-1}) and low residual basal area (6 m^2 ha^{-1}). VPD classes are established according to the 20th, 40th, 60th and 80th percentiles. Diamonds correspond to the mean, central lines are the median, whiskers represent lower or upper values observed within 1.5 times the interquartile range, and black points are outliers.

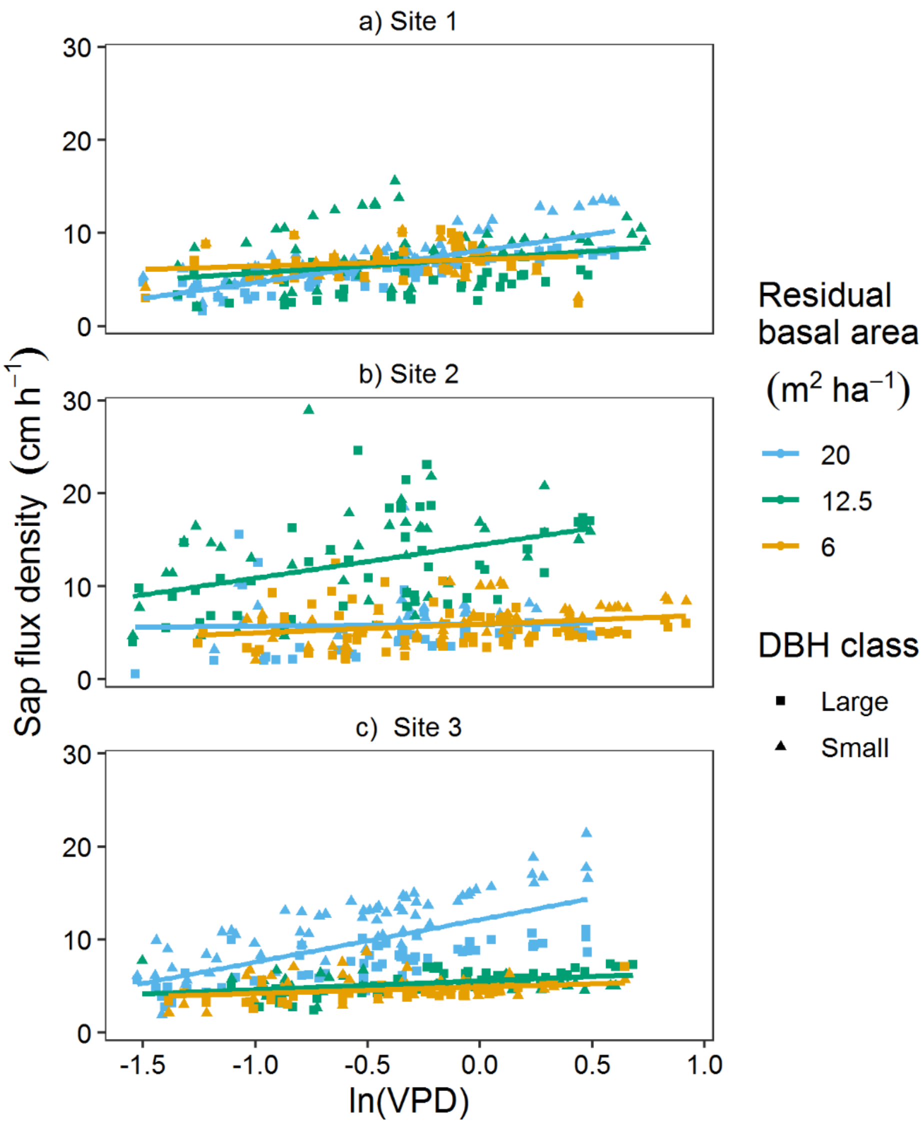

Figure 2.3 Daily sap flux density (Fd, cm h^{-1}) as a function of ln-transformed mean daily vapor pressure deficit (VPD) for a gradient of residual basal area treatments, including high residual basal area (20 m^2 ha^{-1}), medium residual basal area (12.5 m^2 ha^{-1}) and low residual basal area (6 m^2 ha^{-1}). for a) site 1, b) site 2 and c) site 3. Solid lines correspond to regression line for each residual BA. Squares represent trees in the large size class (DBH ≥ 23 cm) and triangles trees in the small size class (9 cm ≥ DBH ≤ 18 cm).

2.4.5 Influence of residual basal area on stand transpiration

Before computing stand transpiration, we tested for the presence of radial variation in Fd to assess whether to include this aspect when upscaling at the stand level. We found that the interaction between the ln-transformed VPD and the sensor position was significant when modelling daily Fd of trees in the large size class (Table S2). The inclusion of radial variation had a considerable influence on estimates of stand transpiration. We found that, on average, stand transpiration was overestimated by 4 % when radial variation was not included.

Figure 2.4 shows total transpiration of stands made up solely of red maple with a residual BA of 20, 12.5, 6.5 m^2 ha^{-1} during the study period (n = 76 days). Total stand transpiration was estimated at 111 mm in the high residual BA plot, 88 mm in the medium residual BA plot and 46 mm in the low residual BA plot. The reduction in residual BA did not translate into a proportional reduction in total stand transpiration. Transpiration at the low residual BA plot amounted to 41 % of the transpiration simulated for the high residual BA plot while the low residual BA treatment had 30 % of the BA of the high residual BA treatment. Similarly, transpiration at the medium residual BA plot amounted to 79 % of the transpiration simulated for the high residual BA plot while the medium residual BA treatment had 63 % of the BA of the high residual BA treatment.

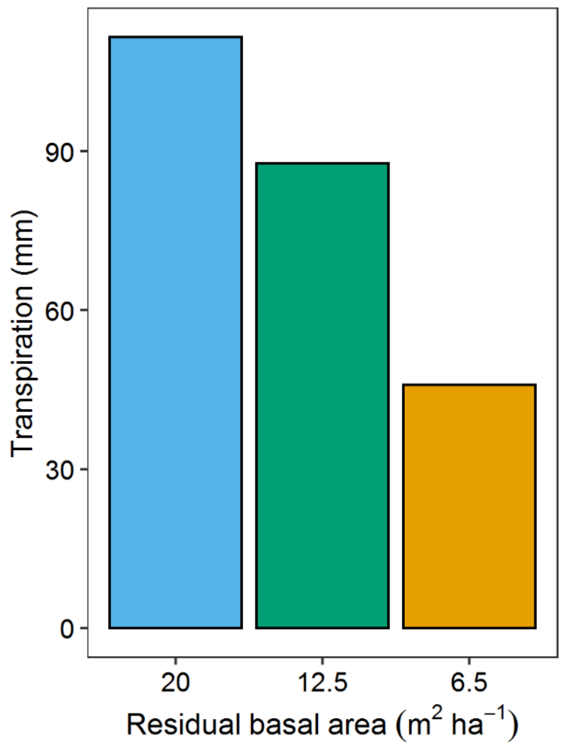

Figure 2.4 Total transpiration simulated for a red maple stand for a gradient of residual basal area treatments, including high residual basal area (20 m^2 ha^{-1}), medium residual basal area (12.5 m^2 ha^{-1}) and low residual basal area (6.5 m^2 ha^{-1}). The period considered was between June 17th and August 31st, 2020.

2.5 Discussion

2.5.1 VPD decreased with residual basal area

Low residual BA promoted drier conditions as shown by a significantly greater VPD in low residual BA plots compared to high residual BA plots (Table 2.2, Figure 2.1). Previous studies have also showed VPD modifications as a result of BA reduction. In a mixed conifer forest in southern California, overstory thinning, which removed more than 50% of the BA (mean initial BA = 59 m2 ha-1, mean residual BA = 26 m2 ha-1), led to a two-fold increase in VPD in post-treatment conditions compared to pre-treatment conditions (Ma et al., 2010). Even a small BA reduction by 14 % (initial BA = 40.9 m^2 ha^{-1}, residual BA = 36 m^2 ha^{-1}) in a *Pinus strobus* stand in southern Ontario led to a 0.3 kPa increase in mean VPD compared to pre-treatment conditions (Skubel et al., 2017).

In the high residual BA plots, the LAI was three times greater than in the low residual BA plots (Table 2.1). A more open canopy is associated with greater incident solar radiation leading to warmer air temperatures when compared to unthinned plots (Trentini et al., 2017; Kermavnar et al., 2020). With less obstacles, wind speed is generally greater in thinned plots compared to control plots (Russell et al., 2018) and Kim *et al*. (2014) found that VPD increase by 11 % for a 1 m s^{-1} wind speed increase in a temperate mixed forest. Overall, warmer air temperatures and greater ventilation generally translate into an increase in VPD in thinned plots (Ma et al., 2010; Gavinet et al., 2015; Tsamir et al., 2019) which is in agreement with our observed decrease in VPD with residual BA.

While VPD was greater in low residual BA plots than in high residual BA plots, medium residual BA treatments had a variable effect on the VPD. Depending on the site, VPD at medium residual BA plots was either similar to the high (site 2) or to the low (site 3) residual BA plots (Figure 2.1). This variation at site level does not appear to be tied to the LAI given similar reduction between plots of each site (Table 2.1). Similarly, tree composition does not appear to explain site level variation, given that site 2 had a mixed composition with coniferous and deciduous tree species, while site 3 mainly comprised deciduous tree species (Table 2.1).

2.5.2 Tree-scale sap flux density increased with residual basal area

We showed that Fd in high residual BA plots was significantly greater than in plots with medium and low residual BA (Table 2.3). The effect varied according to VPD conditions and was most pronounced during days with high VPD (≥ 0.8 kPa, Figure 2.2). This result goes against our hypothesis that a low residual BA would reduce competition for water resources leading to greater Fd at the tree level. Indeed, most research have found a negative relationship between residual BA and Fd. For example, Del campo *et al*. (2014) showed that, during relative warm days (temperature > 13.2 °C) occurring during dry periods (14 consecutive days with precipitation < 5 mm), Fd was significantly lower in high residual BA plot (27.2 m^2 ha^{-1}) compared to medium residual BA (18.2 m^2 ha^{-1}) and low residual BA (9.4 m^2 ha^{-1}) plots in a semi-arid pine plantation. In addition, when thinning treatments of low intensity (13 % to 35 % BA removal) were performed in temperate forests, Fd was also generally greater in thinned plots compared to control plots, either in plantations (Skubel et al., 2017) or in natural forests (Bréda et al., 1995).

In the present study, thinning treatments removed at certain plots more than 70 % of the initial BA (Table 2.1) and the removal of such a large percentage of the initial BA could lead to lower water availability to trees as a result of increased evaporation at the forest floor, either from bare soil evaporation or transpiration from understory vegetation. For example, a 82 % BA reduction in a semi-arid pine forest led to a decrease in soil moisture in the first 30 cm layer (Simonin et al., 2007). In contrast, a small BA removal (14 % of BA removed) and a medium BA removal (50 % of BA removed) have increased soil moisture in conifer forests (Skubel et al., 2017; Ma et al., 2010). In a temperate mixed forest, no differences in soil water content were found between small (20 % of BA removed), medium (40 % of BA removed) or large (60 % of BA removed; Liu et al., 2019) BA removal treatments. Comparable soil water content was also found between a control plot (BA = 28.9 m^2 ha^{-1}) and a thinned plot (residual BA = 22.0 m^2 ha^{-1}), following a 24 % BA removal in a boreal forest (Lagergren et al., 2008). During our study, we had installed soil water content sensors in plots but sensor malfunctioning prevented us from using the data. As such, we could not determine if a low residual BA increased soil water availability. In one of the rare study that measured post-thinning evaporation at the forest floor, a 48 % BA removal through strip thinning in a Japanese cypress plantation led to a two-fold increase in forest floor evaporation (Sun et al., 2016). Thus, reduced soil water availability resulting from an increase in forest floor evaporation could explain the small daily Fd observed in our low residual BA plots.

Additionally, the positive relationship observed between Fd and residual BA is in opposition to what is found in the literature and could possibly be explained by the fact that our study was conducted under climatic conditions close to the norm. Indeed, most studies looking at the response of Fd to thinning focused on drought events (Lagergren et al., 2008; Sinacore et al., 2019), or were conducted in a semi-arid climate (Simonin et al., 2007; del Campo et al., 2014). Under these conditions, water was clearly a limiting factor thus a reduction in BA through thinning initiated a clear increase in Fd. In our study, water was perhaps not the main limiting factor which could explain the large site-level variability in the response of Fd to residual BA. In drought years, the response of Fd at our study sites could potentially be different than what we observed in the present study. More research is needed to gain a better understanding of the response of forests to thinning when water limitations are not severe.

In the present study, we found considerable variability at the site-level regarding the response of Fd to residual BA treatments, thus suggesting the difficulty of prescribing the adequate residual BA to reduce competition for water resource. Indeed, in the medium residual BA plot at site 2 and in the high residual BA at site 3, we measured Fd values that were two times larger than in other plots (Figure 2.3). Site level variability could be tied to various factors. First, differences in soil texture at the site level could have influence Fd. The predominance of sand in a soil reduces its water holding capacity, increasing the sensitivity of trees to heat and drought (Phillips et al., 2016). For example, the Fd of willows growing on loess soil (sand = 52.5 %) was 78 % greater than the Fd of those growing on a sandy soil (sand = 84.2 %) over a two year period (X.Peng et al., 2015). Second, we observed site-level differences in the response of understory vegetation to residual BA treatments. Based on visual observations, understory vegetation appeared sparser in the medium residual BA plot at site 2 and in the high residual BA plot at site 3 compared to other plots. This would result in less competition for water resources which could explain the greater Fd values at these plots (Figure 2.3). However, we did not perform any inventory of understory vegetation to confirm these observations.

2.5.3 Stand-scale transpiration increased with residual basal area

During the first growing season following treatment, stand transpiration estimated for the high residual BA treatment (111 mm) was in line with previous studies located in temperate conditions. In a pine-spruce forest, a thinned stand with a 22 m^2 ha^{-1} residual BA had and estimated transpiration of 159 mm during summer (Lagergren et al., 2008). In the present study, transpiration estimated for the low and medium residual BA treatments represented 41 % and 79 % of the transpiration estimated for the high residual BA treatment. Reduced transpiration in the low BA plot can be tied back to various factors. First, drier conditions observed in low residual BA plots (Figure 2.1) would promote greater transpiration rates in these plots given the positive relationship between Fd and VPD (Figure 2.3). However, this effect was overwhelmed by the reduction in BA and thus the associated reduction in sapwood area which we used to upscale Fd at the tree level (equation 4). In our study, the low and medium residual BA treatments had respectively 30 % and 63 % of the BA of the high residual BA treatment (Table 2.1). Finally, the observed increase in Fd with residual BA (Figure 2.2) likely exacerbated the reduction in transpiration observed in low residual BA treatments. Indeed, a decrease in Fd with residual BA, as typically observed in the literature, would instead have help mitigate differences in transpiration between the different residual BA treatments. Additionally, the reduction in transpiration following thinning treatments could be lessened in the long term given the effect of thinning often fades over time. In some cases, thinned plots have been found to return to transpiration levels close to unthinned plots only two years following treatments (Bréda et al., 1995).

2.5.4 Limitations

Conversion of recorded ΔT into Fd was based on the original Granier equation (Granier, 1987) developed for a coniferous species (*Pseudotsuga menziesii*). While its use to compute Fd of diffuse porous species such as red maple has been validated (Bush et al., 2010), the use of a species-specific equation would improve the estimation of stand transpiration. Furthermore, the use of the Granier equation has little effect when comparing Fd between residual BA treatments given its use on a relative level. Simulated stand transpiration assumed a unique tree species per plot while red maples represented between 50 % and 93 % of the residual BA at our studied plots. Overall, our approach provided a rough estimate of stand-scale transpiration but a larger tree sampling effort as well as Fd measurement of other species (such as *Pinus strobus*, *Tsuga canadensis,* or *Populus grandidentata*) would improve transpiration estimates. While, information on the soil water content would certainly have been useful to assess water availability to trees in thinned plots, soil moisture data would only have been collected in surface soil layers (typically in top 30 cm) whereas mature red maple trees can have a rooting depth of up to 3 m (Abrams, 1998). In this sense, Fd values offer a more integrative variable that reflects the whole tree response to residual BA treatments.

2.6 Conclusion

Very few studies have investigated the response of temperate forests to a gradient of residual BA. This study addressed this gap and described the response of VPD, tree-scale Fd and stand-scale transpiration to three residual BA, that is low (6 m^2 ha^{-1}), medium (12.5 m^2 ha^{-1}) and high (20 m^2 ha^{-1}). While research studying the response of forests to thinning treatments typically focuses on water-limiting conditions (semi-arid climate or drought periods), this study focused on a mesic temperate forest with precipitation generally close to the long-term average during the study period. Moreover, a large number of studies have examined the response of Fd to thinning for coniferous tree species. This study focused on red maple, a deciduous tree species of growing importance due to its great adaptive capacity to climate change (Royer-Tardif et al., 2021). First, we found that VPD decreased with residual BA leading to a greater atmospheric moisture demand in low residual BA plots (Figure 2.1). Second, we had hypothesized that competition for water resources would increase with residual BA which would lead to smaller Fd in plots with high residual BA and greater Fd in plots with low residual BA. However, we found the opposite relationship and contrary to many studies, we found that tree-scale Fd of red maple increased with residual BA, especially during dry conditions (VPD > 1.1 kPa; Figure 2.2). This result may be the consequence of the important BA removal at medium and low residual BA plots (Table 2.1) that may have increase forest floor evaporation, leading to lower soil water availability. Last, we found as expected that red maple stand-scale transpiration increase with residual BA (Figure 2.4).

Overall, we found considerable variability at the site-level regarding the response of Fd to residual BA treatment (Figure 2.3), making it difficult to make recommendations regarding the optimal residual BA required to reduce competition for water resources. A better understanding of post-thinning evapotranspiration by overstory and understory vegetation is needed to better assess the water budget of temperate forest following thinning treatments. Last, long-term Fd monitoring may be the best solution to study the Fd response to a gradient of residual BA. This will allow a better understanding of the response of Fd to different variables like climatic conditions, soil texture and moisture which will help our ability to define the optimal residual BA in temperate forests.

2.7 Acknowledgement

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2.8 Supplementary materials

Table S1: Additional variables tested for the generalized mixed model describing daily sap flux density (Fd) as a function of residual basal area (BA) treatments. Models were tested without the random slope to avoid convergence issue.

		AIC	ΔAIC
	GLMM (Fd)	2999	0
Added variable	Tree diameter at breast height	3008	9
	Plot leaf area index	3013	14
	Plot initial BA	3004	5
	Δ BA*	3003	4
	Daily precipitation	3012	13

*corresponds to the difference in plot BA before and after thinning treatment

Table S2: Generalized mixed model describing daily sap flux density (Fd, cm h^{-1}) as a function of sensor position (outer, inner) for red maple trees of the large size class.

	Estimate	Standard error	*z* value	*p*-value
intercept	1.96	0.11	17.58	**< 0.01**
ln(VPD)	0.09	0.05	1.87	0.06
sensor position outer	-0.10	0.09	-1.17	0.24
ln(VPD) : sensor position outer	0.23	0.03	8.83	**< 0.01**

CHAPITRE III

CONCLUSION

Le but de cette étude était de comprendre comment l'effet de différentes éclaircies forestières influençaient la transpiration d'une espèce d'arbre feuillue (*Acer rubrum*) en forêt tempérée mixte. Les objectifs spécifiques étaient de décrire comment un gradient de surface terrière résiduelle (20; 12,5 et 6 m² ha^{-1}) influençaient les conditions microclimatiques, la densité de flux de sève de l'érable rouge et la transpiration d'un peuplement d'érable rouge. Nous avions fait l'hypothèse que la compétition pour les ressources hydriques augmenterait avec la surface terrière résiduelle, ce qui se traduirait par une densité de flux de sève des arbres supérieures dans des peuplements avec une faible surface terrière résiduelle en comparaison aux peuplements avec une grande surface terrière résiduelle.

Premièrement, nous avons démontré que les conditions microclimatiques sont affectées par un gradient de surface terrière résiduelle. Les valeurs de déficit de tension de vapeur (VPD) sont significativement plus faibles dans les parcelles avec une grande surface terrière résiduelle (20 m² ha^{-1}) comparativement aux parcelles avec une faible surface terrière résiduelle (6 m² ha^{-1}). Ce résultat fut observé pour deux de nos trois sites d'études. Deuxièmement, nous avons montré que la densité de flux de sève (Fd) est significativement plus élevée dans les parcelles avec une grande surface terrière résiduelle comparativement aux parcelles avec une surface terrière moyenne (12,5 m² ha^{-1}) et faible. Le modèle statistique a permis de démontrer que ces différences sont liées aux conditions microclimatiques et sont particulièrement prononcées lors de jours avec un VPD élevé. Par ailleurs, la réponse observée de Fd au gradient de surface terrière résiduelle est fortement variable selon nos sites et nos parcelles. Dernièrement, nous avons montré que la transpiration simulée pour un peuplement d'érables rouges en forêt tempérée était affectée par les éclaircies. La simulation réalisée à partir des données de flux de sève d'érable rouge montre que la transpiration totale dans les parcelles avec une surface terrière résiduelle faible et moyenne correspondait à 41 % et 79 % de la transpiration simulée pour une parcelle avec une grande surface terrière résiduelle. Nous avons aussi démontré qu'il est nécessaire d'inclure la variation radiale de Fd dans le calcul de la transpiration. En effet, les valeurs de Fd sont significativement différentes selon la profondeur d'insertion des senseurs dans le bois d'aubier d'un érable rouge, entrainant une transpiration simulée 4 % plus importante quand la varaition radiale n'est pas incluse.

Les résultats obtenus pour Fd sont contraires à nos prédictions. En effet, notre hypothèse principale stipulait que nous nous attendions à rencontrer des valeurs de Fd plus élevées dans des parcelles avec une faible surface terrière résiduelle. Nous avons observé une relation inverse avec des valeurs de Fd plus élevées dans des parcelles avec une grande surface terrière résiduelle lors de jours secs. Cela suggère que les arbres des parcelles avec une faible surface terrière résiduelle pourraient avoir été restreints dans leur accessibilité à l'eau du fait d'une forte évaporation au niveau du sol et/ou d'une forte transpiration du sous-couvert forestier. Les estimés de transpiration sont en accord avec nos prédictions avec une transpiration simulée plus importante dans la parcelle avec une grande surface terrière résiduelle que dans celle avec une faible surface terrière résiduelle.

La disponibilité et la répartition de l'eau pour les arbres sont deux éléments que nous aurions voulu étudier avec plus de précision. Cependant, les problèmes rencontrés avec un capteur empêchèrent la collecte des données d'humidité et de température du sol. De plus, un dispositif d'exclusion de précipitations n'a pu être mis en place en raison d'un manque de financement et de la pandémie liée au Covid-19. Ce dispositif d'exclusion de précipitation aurait permis de simuler un épisode de sécheresse durant les 76 jours de notre étude. L'objectif aurait été de réaliser une comparaison entre une parcelle non-éclaircie et une éclaircie, pour lesquelles un dispositif d'exclusion de précipitation aurait été installé. Quatre traitements avec différentes conditions hydriques auraient ainsi pu être étudiés : un contrôle (sans éclaircie, ni exclusion), une sécheresse simulée (sans éclaircie mais avec exclusion), une éclaircie (avec éclaircie mais sans exclusion) et une éclaircie avec sécheresse simulée (avec éclaircie et avec exclusion). Ce dispositif nous aurait permis d'observer comment se serait comporté le Fd en période de sécheresse lorsque l'eau aurait été une condition limitante. Ainsi nous aurions pu relier la grande variabilité de réponse de Fd entre parcelles à une condition limitante en eau ou à un autre facteur.

Pour terminer, il serait envisageable de mener un suivi sur le long terme de Fd afin de comprendre son évolution au court du temps. Cela permettrait d'étudier la saisonnalité de Fd ou encore d'observer l'évolution de la réponse du Fd à gradient de surface terrière résiduelle. L'objectif final serait de déterminer quelle serait la surface terrière résiduelle optimale ou encore la période optimale pour réaliser une éclaircie afin d'optimiser l'accès à l'eau pour les arbres en forêt tempérée mixte.

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