

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ADAPTATION ET GESTION DE L'ARBRE SOUS LES RÉSEAUX
ÉLECTRIQUES EN MILIEUX URBAINS : CARACTÉRISATION DES
FACTEURS QUI INFLUENCENT LES RÉPONSES TRAUMATIQUES
POST-INTERVENTION DE TAILLE

THÈSE

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GUILLAUME PERRETTE

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RÉSUMÉ

En fournissant une multitude de services économiques et environnementaux, l'arbre est un élément indispensable dans le paysage urbain. Cependant, l'arbre peut entrer très rapidement en conflit avec les infrastructures humaines, et plus particulièrement avec le réseau de distribution d'électricité avec lequel il partage l'espace aérien. Ainsi, pour préserver la pérennité des installations électriques, mais également pour assurer le bon fonctionnement et la sécurité de celles-ci, l'arbre fait face à une maîtrise de son développement par des interventions de tailles. Pourtant, quelques années après une intervention de taille, l'espace libéré dans la structure interne de la cime de l'arbre est de nouveau colonisé, plus ou moins rapidement, par de nouvelles unités réitératives, nécessitant une planification cyclique d'entretien relativement onéreuse. D'autant plus que ces interventions répétitives peuvent altérer la stabilité mécanique de l'arbre en favorisant le développement de carie au point de coupe et ainsi remettre en question la sécurité du public. Peu d'études ont été menées sur la compréhension des principaux facteurs qui dynamisent ces réponses dans le but d'optimiser les intervalles d'entretien tout en garantissant des arbres sains et sûrs pour le futur. Par conséquent, ce projet avait pour objectif principal de caractériser les principaux facteurs qui affectent et contrôlent l'initiation et le développement des réitérations ainsi que la compartimentation des plaies à la suite d'une intervention de taille afin d'élaborer des recommandations simples qui minimisent les réponses traumatiques tout en maintenant une croissance saine de l'arbre autour des infrastructures électriques. Pour limiter toute influence confondante liée aux conditions environnementales urbaines pouvant avoir un effet sur les réponses de l'arbre à la suite de traitement de taille, tous les dispositifs expérimentaux de cette thèse ont été installés en milieu contrôlé au sein de la pépinière de la ville de Montréal à L'Assomption. De par ses dispositifs expérimentaux, utilisant différents traitements de taille sur des arbres d'une dizaine d'années en milieu contrôlé et visant à améliorer notre compréhension du fonctionnement de l'arbre soumis à une perte d'une partie de sa couronne, ce projet reste unique.

Le premier dispositif expérimental a permis d'évaluer spécifiquement l'influence de l'intensité et de la saison de taille sur les réponses traumatiques de l'arbre à la suite d'une réduction de la tige principale. Des intensités de réduction plus grandes ont entraîné un nombre, une longueur et une biomasse de réitérations plus importantes, ainsi qu'une compartimentation inférieure de la plaie de taille comparativement à des intensités plus faibles. De plus, intervenir durant la période de croissance a limité l'initiation et le développement des réitérations par rapport à une intervention réalisée durant la saison de dormance sans toutefois affecter davantage la compartimentation de la plaie de taille.

Le second dispositif expérimental a été effectué pour analyser l'influence de la vigueur des arbres avant une réduction de la tige principale sur les réponses traumatiques après taille de deux espèces couramment plantées en milieu urbain. Les résultats ont montré que plus un arbre était vigoureux et en bonne santé au moment de la taille, plus il a réitéré au point de coupe après l'intervention. Néanmoins, la capacité de l'arbre à produire des réitérations au point de coupe fut influencée par l'efficacité de l'espèce à compartimenter la plaie de taille. Une capacité de compartimentation moins efficace de la plaie de taille a entraîné une diminution de la production de réitérations.

Enfin, le dernier dispositif expérimental a été élaboré pour examiner l'influence de l'inclinaison de l'appel-sève avant une intervention de réduction de la tige principale de l'arbre sur le processus de restauration du houppier. Des interventions de tailles de réduction de la tige principale réalisées sur des appels-sève plagiotropes ont augmenté l'initiation des réitérations au point de coupe et diminué le recouvrement de la plaie de taille tout en affectant négativement la reprise de l'appel-sève.

En somme, une faible intensité de taille réalisée durant la période de croissance couplée avec un inventaire préalable de l'état sanitaire des arbres pour détecter les arbres les moins vigoureux, tout en prenant soin techniquement de ne pas réaliser les tailles de réduction sur des appels-sève plagiotropes seront garants d'une optimisation des intervalles de retour d'entretien tout en conservant des arbres sains et sûrs autour des réseaux électriques.

Mots clés : Contrôle végétation, taille de réduction, intensité et saison de l'intervention, vigueur et santé de l'arbre, inclinaison de l'appel-sève, réitération, compartimentalisation, optimisation, intervalle de retour d'entretien, réseau électrique.

INTRODUCTION

0.1 Une entité incontournable du paysage urbain : l'arbre

En milieu urbain, la présence d'espaces verts tels que les parcs et les boisés participe activement à l'amélioration de la qualité de vie (Bolund et Hunhammer, 1999; Chiesura, 2004). L'arbre, élément structurel majeur de ces écosystèmes, est également pleinement utilisé au sein même de la conception du tissu urbain (Mollie, 2009). Planté au coin d'une rue, sur une place publique, devant des immeubles, sur une avenue ou sur des terrains privés, l'arbre assure de nombreuses fonctions : il vient parfaire l'orientation, met en valeur un monument, agrmente la rigidité du bâti urbain, brise la rectitude des voies de circulation et enjolive l'espace de détente. De façon moins visible, mais pourtant tout aussi importante, l'arbre est également un véritable poumon vert qui purifie l'air de la ville. Par exemple, en absorbant directement les gaz polluants émis par le trafic routier et les industries (Yang et al., 2005), l'arbre contribue activement à la diminution des risques de problèmes respiratoires (Nowak et al., 2014). Durant les mois d'été, de par son ombrage et sa transpiration, l'arbre améliore la température ambiante en la rafraîchissant et participe de ce fait à la diminution de la formation des îlots de chaleur (Akbari et Konopacki, 2005). En outre, tout au long de son cycle de vie, l'arbre atténue les impacts des changements climatiques en assimilant et en transformant le dioxyde de carbone atmosphérique en biomasse végétale (Nowak, 1993; Nowak et Crane, 2002). Ainsi, en fournissant un large éventail de bénéfices environnementaux, écologiques, sociaux, culturels et économiques, l'arbre n'est pas seulement un élément naturel du paysage, mais également et surtout un élément indispensable dans le paysage urbain pour le bien-être des citoyens.

0.2 Une cohabitation souvent difficile avec les infrastructures urbaines

Devant l'intensification de l'utilisation des terres et la maximisation de celles-ci au profit du développement urbain, l'espace accordé pour le bon développement de l'arbre est souvent minimisé. Ainsi, les arbres, qu'ils se retrouvent isolés ou en groupes, doivent continuellement s'adapter et moduler leur développement pour cohabiter avec les différentes contraintes anthropiques. Bien que l'arbre soit reconnu pour fournir de nombreux bénéfices à la société, il peut cependant entrer rapidement en conflit avec les infrastructures humaines, notamment par l'entremise de ses racines (Randrup et al., 2001) et de ses pousses annuelles, branches et charpentières (Goodfellow et al., 1987) ou présenter des sources de danger remettant en cause la sécurité du public (chute de branches, pousses annuelles qui entrent en contact avec les fils non isolés Réseaux Moyenne Tension [RMT] et déclenchent des feux). Par conséquent, pour préserver la pérennité et assurer le bon fonctionnement des installations, mais également pour assurer la sécurité du public, l'arbre, dans certaines mesures, doit faire face à la taille de ses parties vivantes en vue de maîtriser son développement. Les principaux objectifs de la taille sont donc d'établir et de maintenir des arbres sains, esthétiques et sûrs pour le public et les infrastructures urbaines (Dujesiefken et al., 2016).

0.3 Une cohabitation récurrente de l'arbre avec les réseaux électriques

Une des contraintes anthropiques majeures pour la croissance des arbres dans la plupart des villes nord-américaines concerne le réseau de distribution d'électricité avec lequel l'arbre est souvent en conflit pour l'occupation de l'espace aérien (Dupras et al., 2016). Ainsi, pour diminuer les risques de contact entre les deux entités, qui remettraient en cause le bon fonctionnement du réseau électrique et la sécurité des employés et des utilisateurs, le développement de l'arbre est maîtrisé par l'intermédiaire d'interventions de tailles. Néanmoins, les arbres situés le long des réseaux électriques développent un schéma similaire suite aux tailles de dégagement. Quelques années seulement après

l'intervention, l'espace libéré est de nouveau colonisé, plus ou moins rapidement, par de nouvelles unités réitératives, ce qui implique une planification cyclique d'entretien à intervalle plus ou moins régulier (Goodfellow et al., 1987; Millet et Bouchard, 2003; Follett et al., 2016; Lecigne et al., 2018). D'autant plus, que ces interventions répétitives peuvent altérer la stabilité mécanique de l'arbre en favorisant le développement de zones de faiblesse au point de coupe, et ainsi remettre en question la sécurité du public (Dahle et al., 2006; Dujesiefken et al., 2016).

Chaque année, plus de 800 millions de dollars sont dépensés pour la taille des arbres sous les réseaux électriques aux États-Unis (Goodfellow et al., 1987), contre 60 millions dans la province du Québec au Canada (Millet, 2012). Or, les coûts liés à l'entretien dépendent principalement de la longueur de l'intervalle de retour (régie par le taux de croissance des réitérations), du temps pour tailler un arbre (affecté par le nombre de réitérations à éliminer), de la quantité de biomasse supprimée (associée au volume de réitérations à déchiqeter) (Nowak, 1990; Browning et Wiant, 1997) et de l'espèce d'arbre (Follett et al., 2016). Ainsi, plus l'intervalle de retour est court, plus les dépenses occasionnées sont élevées. Bien que d'un point de vue économique, 5 à 6 ans soit la durée optimale entre deux interventions d'entretien (Browning et Wiant, 1997), le temps de retour peut varier de 3 ans à plus que 5-6 ans à Montréal (Millet et Bouchard, 2003; Millet, 2012; Lecigne et al., 2018). Par conséquent, pour optimiser la maintenance du réseau de distribution d'électricité, les gestionnaires de la végétation ont le défi de produire de bonnes estimations de la repousse des réitérations afin de planifier des retours d'entretien appropriés (Follett et al., 2016). Cependant, les stratégies actuelles d'intervention de taille de la végétation arborée à proximité du réseau de distribution électrique n'intègrent généralement pas ou peu les connaissances propres et connues au bon développement de l'arbre. En effet, à travers les différentes régions du Québec, les retours d'entretien cycles des arbres sont plus souvent planifiés à partir de contraintes administratives et logistiques. De ce fait, la connaissance des réactions de l'arbre à la suite d'une intervention taille est primordiale pour optimiser le temps de retour d'entretien tout en garantissant des arbres sains et sûrs.

Dans la pratique, la recolonisation par réitération de l'espace libéré dans la structure interne de la cime des arbres suite à une taille n'est pas un phénomène nouveau (Meier et al., 2012). Le processus est également perceptible à la suite d'événements écologiques catastrophiques tels que le passage d'un ouragan (Cooper-Ellis et al., 1999), d'une tempête de glace (Brommit et al., 2004), ou d'une taille sévère (Goodfellow et al., 1987; Millet et Bouchard, 2003) lorsqu'une partie voire l'intégralité de la couronne a été endommagée ou détruite, mais aussi dans le cadre d'arbres vieillissants ou sénescents en maintenance de cime (Fay, 2002; Ishii et al., 2007). Ainsi, pour restaurer la couronne endommagée (Deal et al., 2003) et maintenir une balance fonctionnelle entre ses différentes parties (Valentine, 1985), l'arbre tente de rétablir la surface foliaire perdue par l'intermédiaire d'une réponse réitérative traumatique (Millet, 2012).

Cependant, les observations de terrain montrent une grande variabilité dans la réponse traumatique de l'arbre pour rétablir l'équilibre fonctionnel suite à une taille sous les réseaux électriques (Lecigne et al., 2020). Cette variabilité est problématique dans le cas d'Hydro-Québec, car elle affecte directement les intervalles d'entretien. Bien que Meier et al. (2012) ont suggéré que cette variabilité pourrait être influencée voire réglée par différents facteurs endogènes et exogènes, notre compréhension sur ce sujet est encore incomplète compte tenu notamment que l'intervention de taille sous les réseaux électriques est réalisée sur la couronne même des arbres selon des normes bien précises où aucune branche ne doit demeurer à moins de 2,5 et 3 m en dessous et dessus respectivement, et 2 m aux abords des fils conducteurs. Dans ce contexte, cette problématique mérite d'être investiguée au niveau de l'acquisition de connaissances des principaux facteurs intra- et extrinsèques affectant et réglant les réponses traumatiques post-intervention de taille des arbres en milieu urbain. D'un point de vue opérationnel, les résultats obtenus permettront de recommander des actions nécessaires pour améliorer et optimiser les méthodes d'intervention tout en permettant une cohabitation plus harmonieuse avec les infrastructures électriques.

0.4 L'arbre : une stratégie de développement par répétition

L'arbre des milieux tempérés est un organisme modulaire qui, au fil du temps, érige sa structure (tronc, branches et rameaux) selon un nombre limité de règles, programmées génétiquement, et en lien avec sa propre espèce (Millet, 2012). La description de l'architecture d'un arbre repose donc sur la nature et l'agencement relatif de chacune de ses structures dont certaines évoluent en fonction de l'ontogénie de l'arbre et des perturbations subies.

Au cours de ses premières années de vie, l'arbre érige sa première unité de croissance architecturale. Pour chaque espèce des milieux tempérés, la première unité architecturale est composée d'un tronc et d'un nombre fini d'axes ramifiés hautement hiérarchisés et conforme à l'un des 22 modèles architecturaux observés par Hallé et al. (1978). L'axe 1 correspond au tronc, les axes 2 correspondent aux branches directement insérées sur le tronc, les axes 3 correspondent aux rameaux insérés sur les axes 2, et ainsi de suite (Barthelemy et Caraglio, 2007).

Une fois la première unité architecturale mise en place, l'arbre va débiter une série de répliques successives de celle-ci. Ces répliques, appelées répétitions séquentielles, viennent s'ajouter les unes après les autres au fil des années pour ériger le houppier de l'arbre. La forme de l'arbre peut ainsi être décrite comme un empilement d'une colonie d'unités répétées (Hallé et al., 1978). La répétition séquentielle est dite totale si la totalité de l'unité architecturale est dupliquée, ou partielle si une partie seulement de l'unité architecturale est dupliquée.

Néanmoins, en l'absence de traumatisme, une profonde modification des répétitions séquentielles est perceptible chez la plupart des espèces lors du développement du houppier, bien que les répétitions séquentielles peuvent rester conformes à la première unité architecturale chez certaines espèces jusqu'à leur mort en ne formant qu'un seul

tronc (Barthelemy et al., 1995). Ainsi, lors de l'édification du houppier, au lieu de s'intégrer au modèle, certains axes d'ordre 2 ou 3 d'une réitération séquentielle se comportent comme des axes d'ordre 1 ou 2 et reproduisent à leur tour le modèle de base de l'unité architecturale en entier. Ce processus de ramification adaptatif, appelé réitération sylleptique (Raimbault et Tanguy, 1993; Bégin et Filion, 1999) ou immédiate (Bégin et Filion, 1999; Millet, 2012), est à l'origine en partie, chez de nombreuses espèces, de la démultiplication des troncs et des branches maîtresses de l'arbre. La réitération sylleptique ne peut se développer qu'à partir d'un bourgeon axillaire ou terminal n'ayant connu au plus qu'une dormance hivernale (Millet, 2012).

La réitération proleptique (Raimbault et Tanguy, 1993; Bégin et Filion, 1999) ou différée (Bégin et Filion, 1999; Millet, 2012) est quant à elle un autre processus de ramification pouvant modifier la réplique de l'unité architecturale par réitérations séquentielles. À l'opposé de la réitération sylleptique ou immédiate, la réitération proleptique ou différée se développe à partir de bourgeons proventifs axillaires restés latents pour plus d'une dormance hivernale ou à partir de bourgeons adventifs, et ne reproduit que partiellement l'unité architecturale de base. Les réitérations proleptiques ou différées sont également des réitérations adaptatives, mais elles sont localisées principalement sur les branches maîtresses du houppier de l'arbre. Qualifiées d'opportunistes, elles peuvent se développer sans traumatisme apparent (Bégin et Filion, 1999), ou à la suite d'un traumatisme apparent occasionnant une augmentation de l'intensité lumineuse dans le houppier (Bégin et Filion, 1999) ou bien encore dans le cas de renouvellement de la branche lorsque l'arbre est plus âgé (Raimbault et Tanguy, 1993; Fay, 2002; Ishii et al., 2007). Le processus de ramification par réitérations proleptiques ou différées permet ainsi à l'arbre de maintenir la productivité de son houppier et de prolonger par conséquent sa longévité (Ishii et Ford, 2002; Lanner, 2002).

Le dernier processus de ramification pouvant altérer la formation du houppier par réitérations séquentielles concerne la réitération traumatique ou proleptique totale (Raimbault et Tanguy,

1993). Comme son nom l'indique, la réitération traumatique s'initie et se développe à la suite d'événements catastrophiques qui ont endommagé ou détruit la cime de l'arbre (Goodfellow et al., 1987; Cooper-Ellis et al., 1999; Millet et Bouchard, 2003; Brommit et al., 2004), ou dans le cadre d'arbres vieillissants ou sénescents en maintenance de cime (Fay, 2002; Ishii et al., 2007). Tout comme les réitérations proleptiques ou différées, les réitérations traumatiques ou proleptiques totales sont des réitérations adaptatives s'initiant et se développant à partir de bourgeons proventifs axillaires restés latents pour plus d'une dormance hivernale ou à partir de bourgeons adventifs. Cependant, les réitérations traumatiques reproduisent totalement l'unité architecturale de base de l'arbre et se localisent principalement sur le tronc et à la base des branches maîtresses du houppier de l'arbre dans le cas d'arbres vieillissants (Raimbault et Tanguy, 1993) ou proche des blessures dans le cas d'arbres perturbés (Meier et al., 2012).

0.5 De la graine à la sénescence : une croissance et un développement selon une phase d'expansion et de régression

D'une manière générale, depuis sa germination jusqu'à sa mort en l'absence de traumatisme, l'ontogenèse de la vie d'un arbre peut être décrite selon trois grandes étapes de développement distinctes (Hallé et al., 1978). Les deux premières, l'arbre jeune (arbre d'avenir) et l'arbre adulte (arbre du présent) correspondent à une phase d'expansion, tandis que la dernière, l'arbre adulte vieillissant (arbre du passé), correspond à une phase de régression.

Au cours de la première étape de la phase d'expansion, l'arbre jeune est vigoureux et se développe activement. En établissant son architecture élémentaire, l'arbre augmente rapidement la hauteur de son tronc, le volume de son houppier et sa surface foliaire au détriment de la croissance du tronc en épaisseur (Dujesiefken et al., 2016), le tout selon un mode d'organisation simple, très hiérarchisé et peu complexe (Millet 2012; Dujesiefken et al., 2016). Compte tenu d'une dominance apicale très forte de l'axe 1, la forme du houppier

est généralement pyramidale ou conique pointue. Selon les conditions du milieu, l'étape du jeune arbre peut durer plus ou moins de temps (Drénou, 2000a).

Durant la seconde étape de la phase d'expansion, le houppier de l'arbre adulte atteint le volume maximum caractéristique de l'espèce en répliquant sa propre unité architecturale par répétitions séquentielles et par l'intermédiaire de répétitions sylleptiques. L'apparition du processus de répétition est liée à la lente disparition de la dominance apicale et d'une activité hormonale prononcée, mais elle est également due à l'augmentation de l'énergie incidente découlant d'une augmentation de la captation de l'intensité lumineuse induisant un apport de sève accru (Raimbault et Tanguy, 1993). La forme du houppier s'arrondit (Raimbault et Tanguy 1993; Millet, 2012; Dujesiefken et al., 2016), les branches les plus basses s'élaguent naturellement (Raimbault et Tanguy, 1993; Dujesiefken et al., 2016) et le diamètre du tronc croît rapidement (Black et al., 2008). Avec l'apparition des répétitions sylleptiques, le plan d'organisation hiérarchisé rencontré lors de l'étape précédente évolue vers un plan d'organisation plus polyarchique, et donc, plus complexe (Millet, 2012). Au fur et à mesure que l'unité architecturale se réplique, le taux de croissance en longueur et en diamètre de celle-ci diminue progressivement, c'est le phénomène de miniaturisation (Barthelemy et Caraglio, 2007; Millet 2012). De cette manière, en répétant à leur tour, les branches maîtresses issues des répétitions séquentielles ou sylleptiques édifient des branches maîtresses de second ordre de taille plus modeste, et ainsi de suite. Cependant, la diminution successive de la taille des unités architecturales et des branches maîtresses arrive à un tel point que l'arbre met en place progressivement à la périphérie du houppier des unités minimales peu ramifiées et présentant un faible taux de croissance (Barthelemy et Caraglio, 2007; Millet, 2012). L'apparition des unités minimales marque la fin de l'étape de l'arbre adulte, et par conséquent, la fin de la phase d'expansion de l'arbre. L'étape de l'arbre adulte est très longue dans le temps, mais selon les espèces et les conditions de développement, cette étape peut varier fortement.

Lors de la phase de régression, qui correspond à l'étape de l'arbre vieillissant, la formation d'unités minimales s'estompe peu à peu, marquant la fin de la croissance à la périphérie du houppier (Taugourdeau et al., 2019). La croissance du tronc en diamètre diminue (Black et al., 2008) et le volume de l'arbre diminue également (Dujesiefken et al., 2016). Progressivement, les unités minimales mises en place préalablement dépérissent graduellement vers le centre de l'arbre, c'est le phénomène de descente de cime. Le phénomène de descente de cime est également marqué par l'apparition de réitérations proleptiques sur le long des branches maîtresses. Cependant, au fur et à mesure que la descente de cime prend de l'ampleur, de nombreuses branches maîtresses dépérissent, puis se brisent. Un appauvrissement général de la structure de l'arbre occasionné par la dislocation de la cime est ainsi observable. Des réitérations traumatiques s'établissent alors à leur tour de plus en plus bas sur toute la longueur du tronc. Le phénomène de la descente de cime se termine en général par la mort puis la chute de l'arbre.

0.6 Influence des perturbations sur le développement de l'arbre

Dans bien des cas, du stade de jeune tige jusqu'à la sénescence, le développement des arbres n'est pas linéaire et une discordance est observable entre les valeurs de certains paramètres et celles prévues par le standard (Drénou 1999, 2000a). Cette discordance est dans nombre de cas le résultat de l'apparition de réitérations proleptiques ou traumatiques dans le temps à la suite d'événements catastrophiques naturels (sécheresse, gel, tempête de glace, ouragan, épidémie d'insectes) ou anthropiques (taille sévère, blessure sur tronc, excavation du système racinaire). À la suite de perturbations, l'apparition de ces nouvelles structures à différents stades peut considérablement désorganiser l'architecture et le fonctionnement de l'arbre (Millet et Bouchard, 2003) pour l'orienter dans des voies ontogéniques diverses (Figure 0.1; Drénou, 2000a; Dujesiefken et al., 2005b; Drénou et al., 2015).

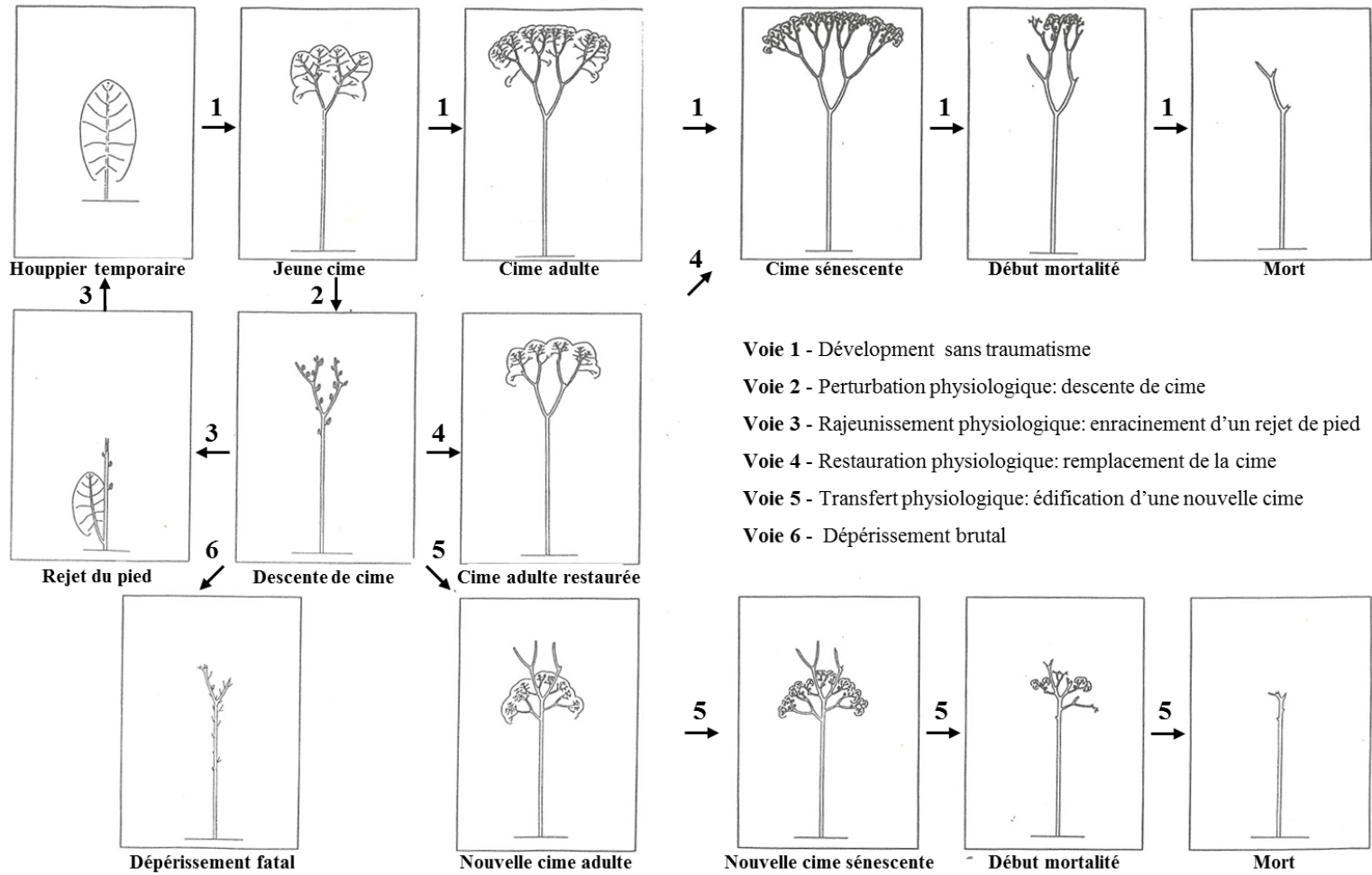


Figure 0.1 Illustration des différentes voies de développement architectural d'un arbre perturbé (adapté de Drénou, 2000a)

0.7 Mécanismes de restauration du houppier de l'arbre après perturbation

0.7.1 Principes du développement des réitérations traumatiques

Chaque année, des bourgeons proventifs axillaires morphologiquement aptes à immédiatement se développer se mettent en place sur les pousses annuelles de l'arbre (Édelin, 1984). Pourtant, dans la très grande majorité des cas, les bourgeons proventifs axillaires ne se développent pas et restent latents, constituant au fil des années une réserve sur les branches et charpentières. Cette inhibition, plus connue sous le terme de dominance apicale lorsque l'arbre est jeune ou contrôle apical lorsque l'arbre est plus âgé, est liée à un contrôle hormonal et est régulée principalement par le ratio entre deux hormones : l'auxine et la cytokinine (Cline, 1994). L'auxine, produite au niveau des jeunes rameaux, est transportée jusqu'aux racines, ce qui a pour effet d'inhiber le développement des bourgeons proventifs axillaires et d'activer la croissance racinaire (Wilson, 2000). Par contre, la cytokinine, synthétisée dans les pointes des racines et transportée dans les parties aériennes, provoque le développement des bourgeons proventifs axillaires (Ongaro et Leyser, 2007). Ainsi, lorsqu'un arbre en équilibre est dépourvu de perturbation et que la partie aérienne de la biomasse est proportionnelle à la biomasse de la partie souterraine, le rapport auxine versus cytokinine est neutre et les bourgeons proventifs axillaires sont au stade latent. Cependant, la suppression ou l'endommagement de la partie aérienne des arbres à la suite d'une perturbation entraîne l'arrêt ou la diminution du transport des auxines des bourgeons vers les racines (Eliasson, 1972). Par conséquent, la dominance apicale ou le contrôle apical sont arrêtés ou diminués (Schier et al., 1985), la concentration en auxine dans les racines diminue rapidement (Eliasson, 1972), et le ratio des cytokinines vis-à-vis des auxines est élevé (Perala, 1990). L'initiation et la croissance des réitérations traumatiques à partir de la levée de dormance des bourgeons proventifs axillaires restés latents peuvent donc débiter (Cline, 2000).

D'un autre côté, l'initiation et le développement des réitérations traumatiques peuvent également être associés à des bourgeons adventifs. À l'opposé des bourgeons proventifs axillaires latents, la formation des bourgeons adventifs est indépendante des pousses annuelles et se réalise toujours post-perturbation (Fink, 1983; Klimesova et Klimes, 2007). Sans connexion vasculaire avec la moelle, les bourgeons adventifs s'initient et se développent proches des zones endommagées, et ce, sur n'importe quelle partie de l'arbre (Fink, 1983; Klimesova et Klimes, 2007).

0.7.2 Facteurs affectant l'initiation des réitérations traumatiques

De nombreux chercheurs considèrent que la dominance apicale ou le contrôle apical sont le principal facteur d'initiation des réitérations traumatiques (Cline, 1997; Del Tredici, 2001). Après une suppression ou un endommagement de la dominance apicale ou du contrôle apical, les réitérations traumatiques s'initient rapidement à la suite de la levée de dormance des bourgeons proventifs axillaires latents ou la formation de bourgeons adventifs (Fraser et al., 2004). La majorité des réitérations prennent position au niveau de l'impact de la blessure sur la partie aérienne (Meier et al., 2012), et ce, de préférence sur les parties exposées au sud et à l'ouest de l'arbre (Collier et Turnblom, 2001; O'Hara et al., 2008). Les dimensions des blessures de taille, lorsque celles-ci sont comprises entre 3,5 cm et 11,4 cm de diamètre sur des chênes de Shumard et de Virginie (*Quercus shumardii* Buckl. et *Quercus virginiana* Mill., respectivement) de 26 à 60 cm de DHP, ne semblaient toutefois pas influencer le nombre de réitérations (Grabosky et Gilman, 2007). Toutefois, la capacité d'un arbre à produire des réitérations à la suite d'une taille est très variable entre les espèces, mais également entre les individus d'une même espèce (Grabosky et Gilman, 2007; Meier et al., 2012). Dans le cas de suppression totale de la dominance apicale (coupe de l'arbre en entier), la plus grande densité de réitérations traumatiques, c'est-à-dire les réitérations basales, est obtenue un an (Frey et al., 2003; Perrette et al., 2014) ou deux ans (Schier et al., 1985) après la coupe totale de l'arbre pour ensuite décroître rapidement durant les huit années qui suivent (Navratil, 1991). Un phénomène

semblable de levée de dormance des bourgeons proventifs axillaires latents ou de formation de bourgeons adventifs s'établit lorsque l'arbre est élagué à des fins sylvicoles pour obtenir des troncs droits dépourvus de nœuds (Waring et al., 2005; O'Hara et al., 2008; O'Hara et Berrill, 2009). Cependant, un manque de littérature est perceptible au regard de l'évaluation de la dynamique temporelle de la densité des réitérations traumatiques initiée à la suite d'une réduction de la dominance apicale au sein même de la cime des arbres.

Collier et Turnblom (2001), Millet et Bouchard (2003), O'Hara et al. (2008), Maurin et DesRochers (2013) ont montré que la densité de réitération était affectée par l'intensité de la taille. De fortes réductions de la masse foliaire induisent une initiation plus forte de la densité de réitération comparativement à des réductions plus faibles. Millet et Bouchard (2003) présumant que la réponse plus forte à l'intensité de la taille est liée au fait que l'arbre tente de rétablir plus vigoureusement la masse foliaire perdue. Ainsi, dans un contexte de sylviculture, pour limiter l'apparition des réitérations, et surtout ne pas trop affecter la croissance de l'arbre, Collier et Turnblom (2001), O'Hara et al. (2008), Maurin et DesRochers (2013) suggèrent que l'intensité de l'élagage ne devrait pas excéder 30 % du volume total de la couronne de l'arbre. Dans un contexte d'arboriculture, Dujesiefken et al. (2016) recommandent de ne pas supprimer plus de 20 % du volume total de la couronne de l'arbre.

La saison de coupe est également reconnue pour être un facteur important au regard de l'initiation des réitérations traumatiques (Gordon et al., 2006; O'Hara et al., 2008; Maurin et DesRochers, 2013). En milieu sylvicole, une remontée de couronne ou une coupe de l'arbre durant la saison de croissance diminue significativement le nombre de réitérations initiées au cours des premières années suivant l'intervention, et ce, par rapport à une intervention réalisée durant la période de dormance (Stoekeler et Macon, 1956; Kays et Canham, 1991; O'Hara et al., 2008; Maurin et DesRochers, 2013). Cependant, au cours de la saison de croissance, la littérature n'est pas précise sur

l'époque qui favorise la plus faible production de réitérations. Par exemple, lorsque les branches basses d'un arbre sont élaguées, Maurin et DesRochers (2013) ont observé sur des peupliers hybrides (*Populus sp.*) de trois ans une plus faible densité de réitérations après une intervention de taille réalisée en début d'été, au moment où les feuilles ont atteint leur pleine expansion comparativement à une taille de fin d'automne lorsque les feuilles sont tombées. Tandis que O'Hara et al. (2008) n'ont observé aucune différence entre des élagages de même intensité réalisés sur des séquoias géants (*Sequoiadendron giganteum* (Lindl.) Buchh.) de 12 ans à différents moments de la saison de croissance.

En milieu forestier, de nombreuses études ont souligné l'importance de la vigueur des arbres pour produire des réitérations (O'Hara et Valappil, 2000; Deal et al., 2003; Colin et al., 2008). Des arbres dominés, dont la croissance radiale est faible, présentent une tendance à réitérer plus fortement que des arbres dominants ou codominants (Meier et al., 2012). Dans ce contexte, la faible vigueur est occasionnée par une forte compétition entre les arbres évoluant dans des peuplements denses (Colin et al., 2010). Néanmoins, l'altération de la vigueur des arbres peut également être occasionnée par d'autres stress liés à des dommages impactés sur la structure même de l'arbre. Ainsi, des blessures sur les racines (Vasiliauskas, 2001), sur le tronc (Neely, 1988) ou dans la couronne (Pisaric et al., 2008) sont reconnues pour affecter négativement la vigueur des arbres. Waring (1987) suggère que la diminution de vigueur observée à la suite de stress est en partie due à une réallocation des réserves pour parvenir à compartimenter les blessures et maintenir les processus physiologiques au niveau requis. Pourtant, la densité de réitération est influencée positivement selon la quantité de réserves stockée dans les structures vitales de l'arbre (Kays et Canham, 1991). Cependant, dans le cas d'arbres non contraints à une pression de compétition et sujets à une réduction de la dominance apicale, aucune étude n'a encore évalué le potentiel de réitération en fonction d'un degré variable de vigueur occasionné par des blessures sur les racines, le tronc ou les feuilles.

0.7.3 Facteurs affectant la croissance des réitérations traumatiques

En parallèle, le potentiel de croissance en longueur des réitérations traumatiques présente une tendance similaire avec celui de la densité de réitérations. En effet, le potentiel d'élongation annuel des réitérations traumatiques présente des différences notables inter- et intra-espèces (Goodfellow et al., 1987; Follett et al., 2016; Lecigne, 2020). De surcroît, le potentiel d'élongation annuel des réitérations traumatiques décline année après année (Goodfellow et al., 1987; Follett et al., 2016; Lecigne, 2020). Dans le cas d'arbres taillés sous les réseaux électriques, la croissance des réitérations traumatiques est en général plus vigoureuse lorsque celles-ci sont initiées dans les parties basses de l'arbre ou que le diamètre des charpentières porteuses est plus important (Millet et Bouchard, 2003; Follet et al., 2016). En outre, lorsqu'une seule partie de la couronne de l'arbre a été perturbée, le potentiel de croissance des réitérations traumatiques est supérieur à celui des réitérations séquentielles (Millet et Bouchard, 2003; Lecigne, 2018).

Tout comme pour l'initiation des réitérations, élaguer ou couper un arbre durant la période de dormance favorise la croissance des réitérations traumatiques initiées sur tronc ou sur souche (Kays et Canham, 1991; O'Hara et al., 2008; Perrette et al., 2014). Kays et Canham (1991) suggèrent que la différence de croissance des réitérations traumatiques sur souche peut être attribuée à un différentiel de réserves stockées utilisables et nécessaires pour l'élongation. En effet, intervenir durant la saison de croissance au moment où les réserves stockées sont faibles, car elles sont utilisées pour la pousse annuelle et la croissance radiale du bois, limite le potentiel d'élongation des réitérations traumatiques sur souche. Par contre, l'élongation est plus vigoureuse à la suite d'une intervention réalisée en période de dormance lorsque toutes les réserves sont emmagasinées dans les racines (DesRochers et al., 2002). Bien que les différences moyennes de la croissance en fonction de la saison ne soient significatives que pendant les deux ou trois années suivant l'intervention, la différence de hauteur totale entre les plus grandes réitérations traumatiques sur souche peut perdurer au-delà de trois ans

(Kays et Canham, 1991; Perrette et al., 2014). Pourtant, aucune information n'est disponible sur le potentiel d'élongation des réitérations à la suite d'une réduction de la dominance apicale en fonction des saisons.

Finalement, le type d'exécution des plaies de taille est l'un des facteurs techniques les plus importants qui influence significativement la production des réitérations lors d'une réduction de la dominance apicale ou du contrôle apical d'un arbre, c'est-à-dire la taille de réduction (Goodfellow et al., 1987; Follett et al., 2016; Lecigne, 2020). Une taille dite directionnelle, c'est-à-dire sur appel-sève, dont le diamètre est égal ou supérieur à 1/3 du diamètre de la branche taillée (protocole de American National Standards Institute [ANSI], 2008), est reconnue pour faire diminuer la production des réitérations, tandis qu'une taille dite d'étêtage, c'est-à-dire ne comportant aucun appel-sève au niveau de la plaie de coupe, a un effet inverse en termes de réitération (Goodfellow et al., 1987; Fini et al., 2015; Follet et al., 2016; Lecigne, 2020). D'un autre côté, la reprise de l'appel-sève est favorisée lorsque l'inclinaison de l'appel-sève avant intervention est plus verticale (Wareing et Nasr, 1961). Pourtant, un manque d'information est observable concernant l'influence de l'inclinaison de l'appel-sève avant intervention sur la réponse réitérative.

0.8 Mécanismes internes de résistance aux blessures après perturbation

À la suite d'une perturbation, les blessures occasionnées sur les parties de l'arbre engendrent une mise à nu des tissus dont la conséquence néfaste principale est de provoquer des infiltrations d'air dans la structure interne (Rayner, 1993). Ces infiltrations d'air vont engendrer instantanément un dysfonctionnement des tissus conducteurs (Kuroda, 2001) par la formation d'embolies (Tyree et Sperry, 1989). L'embolisation des tissus conducteurs va induire une réduction des flux de sève et un changement de l'allocation des ressources qui, à terme, pourra se traduire par une diminution de la vigueur des arbres (Oliva et al., 2010, 2012).

Conjointement, la mise à nu des tissus par des blessures a pour conséquence néfaste de créer une voie d'entrée pour les agents pathogènes. Avec le temps, la dispersion des agents pathogènes dans la structure interne induira la formation de cavités susceptibles d'altérer la tenue mécanique des arbres. Pour faire face à leurs progressions, l'arbre tente de les isoler en les conditionnant au sein même de sa structure par l'intermédiaire d'un processus appelé compartimentation. Ce procédé, décrit par Shigo et Marx (1977) et plus connu sous le nom CODIT (Compartmentalization of decay in trees), s'établit par la mise en place de quatre barrières de protection. Les trois premières barrières de protection formées dans le bois existant visent à s'opposer à la progression longitudinale, centrale et latérale de l'agent pathogène dans les tissus de la structure de l'arbre. La dernière, la plus importante, développée sur le pourtour de la blessure à partir de nouveaux tissus, vise à terme à refermer la plaie en formant un cal de cicatrisation. Compte tenu du fait que l'arbre ne régénère pas les tissus blessés et infectés, la zone compartimentée se décolore au fil du temps (Shigo, 1986) et reste présente dans la structure interne de l'arbre pour toute sa durée de vie.

D'une manière générale, la capacité d'un arbre à compartimenter ses blessures varie selon les espèces (Grabosky et Gilman, 2007). Pour certaines, de solides barrières sont mises en place très rapidement après une perturbation. Pour d'autres, au contraire, le processus est plus lent, ce qui engendre une décoloration du bois plus profonde. Par exemple, à la suite d'une blessure, le chêne de Shumard (*Quercus shumardii*) est reconnu pour compartimenter de manière cinq fois plus efficace que le chêne de Virginie (*Quercus virginiana*; Grabosky et Gilman, 2007). Ainsi, les espèces peuvent être divisées en deux catégories bien distinctes selon leur efficacité à compartimenter (Drénou, 1999; Dujesiefken et Stobbe, 2002; Dujesiefken et al., 2005b, 2016; Grabosky et Gilman, 2007; Gilman, 2011). D'un autre côté, chez les arbres adultes, plus la dimension d'une plaie est importante, plus la compartimentation nécessite du temps (Dujesiefken et Stobbe, 2002). Par conséquent, la zone de décoloration du bois est plus étendue et le risque que l'agent pathogène se propage est augmenté

(Dujesiefken et Stobbe, 2002). En outre, plus le ratio du diamètre de la branche coupée versus le diamètre du tronc à l'insertion de la branche coupée augmente, plus la zone de décoloration est importante (Eisner et al., 2002a; Gilman et Grabosky, 2006). Une tendance similaire est observable lorsque l'arbre est sujet à une réduction de sa hauteur par une coupe directionnelle (Grabosky et Gilman, 2007).

La capacité d'un arbre à compartimenter est fortement influencée par la saison au cours de laquelle la blessure est réalisée (Leben, 1985; Dujesiefken et al., 2005a, 2016; Lee et Lee, 2010). En effet, Dujesiefken et al. (2005a), ont démontré qu'une plaie occasionnée sur une partie du tronc durant la saison de croissance présentait une surface de bois décolorée moins importante ainsi qu'un pourcentage de recouvrement plus important comparativement à une plaie réalisée durant la période de dormance. Dans son étude, Leben (1985) a souligné que la compartimentation et le recouvrement d'une blessure sur tronc sont plus efficaces au début de la saison de croissance (printemps) qu'en toute fin (automne) et présumait que cette différence est reliée à une activité cambiale plus forte en début de saison. Finalement, Lee et Lee (2010) suggèrent que la taille des branches en milieu ou en fin d'été permet un meilleur recouvrement ainsi qu'une plus faible décoloration du bois comparativement à une intervention réalisée en fin d'automne.

La compartimentation est également corrélée avec la vigueur de l'arbre. Plus la croissance en diamètre de l'arbre est importante, plus le recouvrement d'une blessure est rapide (O'Hara et Buckland, 1996; Petruncio et al., 1997; Nicolescu et al., 2013; Sheppard et al., 2016). Pour une même dimension de blessure, un arbre jeune recouvre plus efficacement qu'un arbre adulte (Mercer, 1982). Cependant, la compartimentation semble moins effective lorsque l'arbre est sujet à des stress (Wargo, 1977).

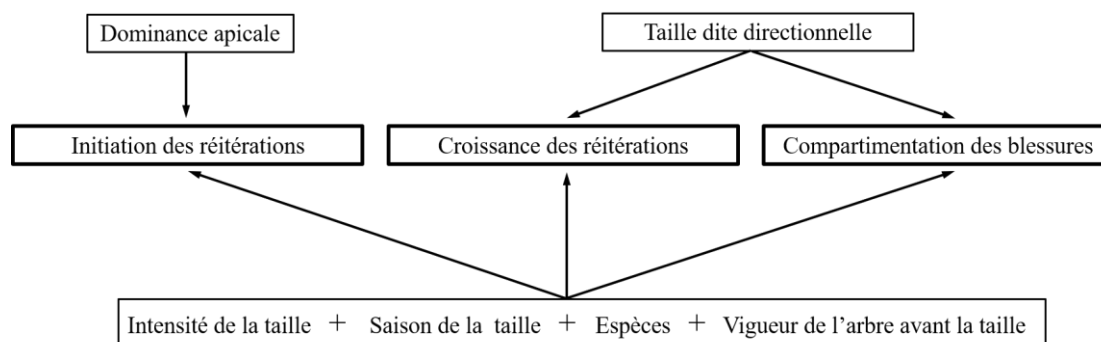


Figure 0.2 Résumé des principaux facteurs qui influencent les réponses traumatiques post intervention de taille

0.9 Vers une optimisation des interventions d'entretien sous les réseaux électriques

Dans un contexte de maîtrise de la végétation sous les réseaux électriques, la suppression par réduction d'une partie de la couronne des arbres provoque l'apparition spontanée et vigoureuse de réitérations traumatiques tout en induisant des faiblesses mécaniques au point de coupe. Ces réponses traumatiques de l'arbre sont problématiques puisqu'un entretien récurrent et coûteux est nécessaire pour tenter de maintenir un degré faible de contact vis-à-vis des réseaux électriques et garantir la sécurité vis-à-vis du public. Pourtant, peu de recherches se sont penchées sur la compréhension des principaux facteurs qui dynamisent ces réponses traumatiques conjointes pour les minimiser et optimiser les intervalles de retour entretien, tout en maintenant des arbres sains et sûrs pour le public. Les résultats, parfois contradictoires, présentés jusqu'à maintenant et issus du domaine sylvicole, illustrent que notre compréhension sur les réponses de l'arbre post-intervention de taille est encore incomplète et que les comparaisons doivent pouvoir se faire avec des facteurs comparables. Les tailles sylvicoles ont pour spécificité de supprimer les branches basses de l'arbre, celles qui au fil des années avec la croissance de l'arbre disparaîtront naturellement. Or, les tailles dites de réduction sont exécutées pour rediriger la croissance de l'arbre, ce qui est aggravant par rapport à une taille sylvicole puisqu'elles

réduisent la dominance apicale, et par conséquent le houppier définitif. Par conséquent, ce projet avait pour objectif principal de caractériser les principaux facteurs qui affectent et contrôlent l'initiation et le développement des réitérations ainsi que la compartimentation des plaies à la suite d'une intervention de réduction de la tige principale de l'arbre afin d'élaborer des recommandations simples qui minimisent les réponses traumatiques tout en maintenant une croissance saine de l'arbre autour des infrastructures électriques.

Le premier volet de cette thèse a porté sur l'influence de l'intensité et de la saison de taille sur les réponses traumatiques de l'arbre. Étant donné qu'il est bien connu qu'une plus grande intensité de taille en milieu sylvicole produit un nombre, une longueur et une biomasse supérieure de réitération (O'Hara et al., 2008; DesRochers et al., 2015), le premier objectif était de déterminer l'ampleur de cet effet à l'échelle d'une réduction de la tige principale chez le frêne de Pennsylvanie (*Fraxinus pennsylvanica* Marsh.). Comme la saison de taille peut également influencer les réponses réitératives en milieu sylvicole (O'Hara et al., 2008; DesRochers et al., 2015), le deuxième objectif était d'évaluer les avantages de réduire la tige principale pendant la saison de croissance par rapport à la saison de dormance. Basé sur la saisonnalité des réserves en carbone que l'on connaît déjà (Kays et Canham, 1991; Furze et al., 2018), la réponse réitérative différera entre les saisons de taille car les opérations seront réalisées à un moment où les réserves seront faibles et l'autre où elles seront importantes. Enfin, le dernier objectif était d'étudier l'influence de l'intensité et de la saison de taille sur la compartimentation des plaies de taille. Compte tenu que l'activité cambiale varie au cours de l'année (Meier et al., 2012), la compartimentation des plaies de taille variera entre les saisons de taille car les opérations seront réalisées à un moment où l'activité cambiale est arrêtée et l'autre active.

Le second volet s'est concentré sur l'influence de la vigueur des arbres avant taille sur les réponses traumatiques post-intervention. L'objectif était d'étudier les réponses

traumatiques de deux espèces couramment utilisées en milieu urbain dans l'est de l'Amérique du Nord à la suite d'une réduction de la tige principale le long d'un large gradient de vigueur. Pour obtenir ce gradient, les micocouliers (*Celtis occidentalis* L.) et les frênes de Pennsylvanie (*Fraxinus pennsylvanica* Marsh.) utilisés ont été soumis à différents types et intensités de stress sur les racines, feuilles et troncs quatre ans avant l'intervention de taille. Compte tenu que les réponses traumatiques sont influencées par les quantités de réserves disponibles (Kays et Canham, 1991) et par la vigueur des arbres (Colin et al., 2010) les réponses traumatiques différeront entre les arbres car les différents stress seront occasionnés à différentes intensités. Un second objectif était d'évaluer comment différents types et intensités de stress ont influencé les réponses traumatiques post-intervention de taille. Lorsque l'arbre est dépourvu de stress, sa balance fonctionnelle entre la partie aérienne et souterraine est à l'équilibre (Valentine 1985). Une diminution du système racinaire implique que l'arbre aura moins besoin de faire de photosynthèse pour maintenir sa biomasse en vie (Sprugel et al., 1991; Lacoite, 2000) d'où une diminution des réponses traumatiques à la suite d'une réduction de sa tige principale.

Finalement, l'objectif du dernier volet était d'examiner l'effet de différentes intensités et saisons de taille de réduction de la tige principale sur la croissance secondaire et la reprise de l'appel-sève post-intervention chez le frêne de Pennsylvanie (*Fraxinus pennsylvanica* Marsh.), mais également d'évaluer l'influence de l'inclinaison de l'appel-sève avant la taille sur la reprise de l'appel-sève, la production de réitérations et la compartimentation des plaies de taille. La résistance à la conduction de l'eau étant dépendante de l'inclinaison de l'appel (plus l'appel sève est orthotrope plus la conduction est importante, Eisner et al., 2002b), les réponses traumatiques différeront car les appels sève avant les opérations de réduction de la tige principale auront des inclinaisons différentes.

L'entièreté de cette thèse s'est déroulée à la pépinière de la ville de Montréal à L'Assomption afin de contrôler toutes influences confondantes associées aux conditions environnementales urbaines pouvant avoir un effet sur la croissance des arbres (Jutras et al., 2010),.

CHAPITRE I

OPTIMIZING REDUCTION PRUNING OF TREES UNDER ELECTRICAL LINES: THE INFLUENCE OF INTENSITY AND SEASON OF PRUNING ON EPICORMIC BRANCH GROWTH AND WOUND COMPARTMENTALIZATION

Perrette, G.^{1,2,3}, Delagrangé, S.^{2,3}, Messier C.^{1,2,3}

¹ Department of Biological Sciences, Université du Québec à Montréal, Centre Ville Station, P.O. Box 8888, Montreal, Qc, H3C 3P8, Canada

² Institute of Temperate Forest Sciences, Université du Québec en Outaouais, 58 Rue Principale, Ripon, Qc J0V 1V0, Canada

³ Center for Forest Research, Université du Québec à Montréal, Centre-ville Station, P.O. Box 8888, Montréal, Qc, H3C 3P8, Canada

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1.1 Abstract

Reduction pruning of the main stem is commonly used during the maintenance of power lines to encourage the establishment and development of scaffold limbs away from wires. Understanding the physiology of epicormic branch initiation and growth as well as wound compartmentalization following reduction pruning are important for optimizing the pruning cycle and maintaining healthy and safe trees. In this study, the influence of both intensity and time of year of pruning on epicormic branch response and wound compartmentalization was investigated on 56 eleven-year-old Pennsylvania ash trees (*Fraxinus pennsylvanica* ‘Marsh’) about 5- to 7-m in height within a controlled nursery environment. During the second growing season following reduction of the main stem, the number, height, and volume of epicormic branches, as well as tallest epicormic branches, and the area of discolored wood increased with pruning intensity. Pruning during the leaf-on season compared to the leaf-off season limited the establishment and development of epicormic branches without affecting wound closure rate or the area of wood discoloration at the cutting point. Results are consistent with the known seasonal fluctuation of carbohydrates reserves. In the context of the electrical distribution network, where trees are subjected to pruning throughout the year, trees pruned in summer during a maintenance cycle could be pruned during the next cycle, in winter, and so on, to optimize the return interval of the pruning cycle.

Keywords: CODIT, Electricity Distribution Networks, Pruning Return Cycle, Sucker Growth, Utility Arboriculture, Vegetation Management.

1.2 Introduction

In urban areas, trees actively contribute to the improvement of human health and quality of life by providing numerous ecosystem services (Bolund and Hunhammar, 1999; Nowak et al., 2018). However, trees are subjected to several pruning operations during their life spans to secure urban infrastructure (Gilman, 2011). Good or better pruning practices will guarantee safety and service benefits of urban trees (Raimbault and Tanguy, 1993; Raimbault et al., 1995; Drénou, 1999; Gilman, 2011; Dujesiefken et al., 2016).

Electricity distribution networks are one of the major utilities in a city that requires continuous pruning maintenance of the tree crown to enhance cohabitation and ensure the safe functioning of the power lines (Dupras et al., 2016). During the mature phase of the tree lifespan (Dujesiefken et al., 2016), tree-crown architecture depends on the planting distance to utility wires and the height and types of utility wires (Millet and Bouchard, 2003; Gilman, 2011). When trees are planted directly under the wire, reduction pruning of the main stem during tree training is commonly used to encourage the occurrence and establishment of scaffold limbs near the cutting point (Millet and Bouchard, 2003; Gilman, 2011). Afterwards, scaffold limbs are directed away from the wire by directional pruning to obtain a "V" bilateral crown form (Millet and Bouchard, 2003; Gilman, 2011; Lecigne et al., 2018). Generally, the first scaffold limb is located between 2 and 4 m from the ground for wires running about 7 to 9 m above the ground (Millet and Bouchard, 2003) because reduction pruning of the main stem is often performed when the annual growth of the terminal shoot comes in contact with the wire (Gilman, 2011). Current knowledge on reduction pruning of the tree main stem suggests that the cut should be made just beyond a scaffold branch and that the diameter of the removed part should comprise between half and two-thirds of the scaffold branch to stimulate the recovery of the apical dominance by this scaffold branch (Gilman and Lilly, 2002; see Figure 1 in Grabosky and Gilman, 2007). Nonetheless, a few years

after reduction pruning, the space created within the internal tree structure is usually filled with epicormic branch recolonization (Goodfellow et al., 1987; Millet and Bouchard, 2003; Follett et al., 2016). The epicormic branch initiation process, originating from proventitious or adventitious buds (Meier et al., 2012), occurs primarily to rebuild the leaf area loss of the crown (Deal et al., 2003) and restore the energy balance between both the above- and below-ground systems following an injury (Valentine, 1985). It is necessary to plan cyclical tree pruning to remove these epicormic branches entering the security corridor beneath the power lines (Millet and Bouchard, 2003; Follett et al., 2016; Lecigne et al., 2018).

Each year, more than 800 million dollars are spent for line clearance pruning in the United States (Goodfellow et al., 1987) compared with 60 million in the province of Québec, Canada (Millet, 2012). These costs of tree maintenance depend on the length of the return interval, the time a tree is pruned, and the amount of biomass removed (Nowak, 1990; Browning and Wiant, 1997). In Montreal, the return time for tree maintenance can vary from three or more years (Millet and Bouchard, 2003; Millet, 2012; Lecigne et al., 2018) depending on the growth rate of the tallest epicormic branch (Follett et al., 2016) although 5 to 6 years is the optimum length of time based on economics (Browning and Wiant, 1997). Therefore, as higher expenses are incurred with shorter intervals, a better understanding of epicormic branch growth rate is needed in order to increase the return time interval and optimize maintenance of the distribution network.

On the other hand, pruning creates wounds and dysfunctional wood at the cutting point and may provide an entry for microorganisms of decay that, over time, can induce cavity formation and alter the health, mechanical strength, and safety of the tree (Dujesiefken and Stobbe, 2002; Dujesiefken et al., 2016). The wound compartmentalization process has been well defined ever since the CODIT (Compartmentalization of decay in trees) model was established by Shigo and Marx

(1977). Following an injury in functional sapwood, trees react by surrounding it with four walls laid down in the wood (Shigo and Marx, 1977; Gilman, 2011). Although walls 1 to 3 prevent the spread of discoloration and decay in the internal wood structure by forming a reaction zone around the wound site, wall 4 closes the exposed wound area over time by forming a protective barrier zone. An increasing number of studies on the compartmentalization process that occurs when a branch is removed have been carried out (Dujesiefken and Stobbe, 2002; Gilman and Grabosky, 2006; Dănescu et al., 2015). However, few studies have focused on tree response to branch (Grabosky and Gilman, 2007) or main-stem reduction (Gilman and Grabosky, 2006).

This study was undertaken to specifically investigate the predominant factors that control the growth-rate response of epicormic branches following a main-stem reduction and their influence on wound compartmentalization. Epicormic branch establishment and development have been extensively investigated in forestry management for stand regeneration after harvesting or for pruning of the lower primary branches in order to improve bole value (Meier et al., 2012). As it is well documented that higher stand basal area prior to harvesting (Kays and Canham, 1991; Babeux and Mauffette, 1994; Perrette et al., 2014) and higher pruning intensity (O'Hara et al., 2008; DesRochers et al., 2015) produce a greater number, length, and biomass of epicormic branches, our first objective was to determine the magnitude of this effect at the tree main stem reduction scale. As the timing of silvicultural operations can also influence the epicormic branch response (Kays and Canham, 1991; Babeux and Mauffette, 1994; O'Hara et al., 2008; DesRochers et al., 2015), our second objective was to evaluate the benefits of main-stem reduction during the leaf-on season versus the leaf-off season. Our final objective was to investigate the influence of the intensity of reduction pruning and time of year on the closure rate and the area of wood discoloration of the pruning wound. To avoid urban environmental conditions that could affect tree growth (Jutras et al., 2010), this study was carried out within a controlled nursery environment.

1.3 Material and methods

1.3.1 Study site

The study was conducted 40 km northeast of Montréal at the Montréal Municipal Nursery in Assomption, Québec, Canada (45°48'N 73°25'W). In this area, the climate is continental and humid, with hot summers and cold winters. The mean annual temperature is 5.3°C and the mean annual precipitation is 1018.7 mm with a mean annual snow cover of 208.9 cm (Environment Canada 2018, Assomption weather station). The soil is clay and clay mixed with fine sand subsoil.

1.3.2 Experimental design and pruning treatments

The experiment took place in 2015 in an existing plantation composed of two cultivars of Pennsylvania ash trees (*Fraxinus pennsylvanica* Marsh.) from field-grown seedlings propagated in 2004 and transplanted in 2009. A total of 21 and 35 trees from 'Prairie Spire' and 'Patmore' cultivars, respectively, devoid of stress were selected among 22 and 39 individuals, respectively (see explanation below for selection). Trees from 'Prairie Spire' were 6-6.6 m in height and 7.7-9.4 cm in DBH, whereas the 'Patmore' attains a height of 5.6-7.3 m and a DBH of 5.7-9.7 cm.

The experiment consisted of 7 treatments, arranged in a random block design with 3 and 5 blocks (replicates) for 'Prairie Spire' and 'Patmore' cultivars, respectively, and 7 trees per block. In addition to control with no reduction pruning treatment, 2 main-stem reduction pruning treatments were performed between 2 and 2.5 m as well as between 3 and 3.5 m above the ground (hereafter referred to as high and low intensity of reduction pruning, respectively) to simulate a prescribed corridor zone of 2.5 m around a fictitious power distribution network located 7 m above the ground, during 3 distinctive season periods : early July, early September, and early December (hereafter referred to as

summer, late summer, and winter, respectively). As the retained scaffold branch diameter relative to the parent axis diameter (aspect ratio) affects the surface area of decay after pruning (Eisner et al., 2002; Gilman and Grabosky, 2006), we tried to keep the aspect ratio of the main stem reduction pruning across trees within a small range (from 0.38-0.46). Although, control trees were not pruned, they had one similar aspect ratio between trunk and a scaffold branch in each part located between 2 and 2.5 m as well as between 3 and 3.5 m above the ground than for pruned trees. To obtain the range of aspect ratio between trunk and scaffold branch in pruned and control trees, similar unions were first selected on each tree for both intensities of reduction pruning and prior to assigning random block treatment. For each branch union selected, the trunk and scaffold branch diameters were measured 10 mm above the scaffold branch bark ridge with a 2-m Lufkin tape measure to determine the aspect ratio of the main stem reduction pruning. Trees with no aspect ratio that ranged from 0.38 to 0.46 for both intensities of reduction pruning treatments were excluded from the study. Trees with aspect ratios for both intensities of reduction pruning treatments were conserved as controls and not pruned, whereas season treatments were randomly assigned to trees on which only one intensity of reduction pruning was applied. For each reduction pruning treatment of the main stem, only one reduction pruning cut was made using a hand saw so as to comply with the American National Standards Institute (ANSI, 2008). Pruning wound diameters ranged from 5 to 7.5 cm and from 4.2 to 6.6 cm for high and low intensity of reduction pruning treatments, respectively. The amount of biomass removed was visually estimated by two assessors and ranged from 60 to 72% for the high intensity of reduction pruning treatment and from 35 to 52% for the low intensity of reduction pruning treatment. Including the retained scaffold branch of the main stem reduction pruning, 4 to 6 and 10 to 15 lateral branches remained on the trunk for high and low intensity of reduction pruning treatments, respectively. No reduction pruning treatment of the main stem was made on a scaffold branch with included bark or codominant aspect and no heartwood was visually present on any reduction pruning cut.

1.3.3 Data collection

1.3.3.1 Epicormic branch inventory

Live epicormic branches from each tree were counted and measured during late summer from 2015-2017. As defined by Bégin and Filion (1999), all deferred or proleptic epicormic branches on the trunk and branches were counted. Additionally, all immediate or sylleptic epicormic branches on branches were counted (except in 2015) if their annual growth length was greater than the annual growth length of the retained scaffold branch of the main stem reduction pruning. Each inventoried epicormic branch was first labeled using a tapener, measured for initiation height, and classified relative to the year of its establishment, i.e., 2015, 2016, or 2017. All the growth units of each epicormic branch were classified per branching order (Barthelemy and Caraglio, 2007). The length was recorded with a ruler and the median diameter was recorded with calipers at the widest part and at right angles for an average rounded to the nearest mm. To obtain the total height and volume per epicormic branch, growth units of primary order lengths and growth unit volume of all branch orders were added. Growth unit volume (V) was calculated according to the formula:

$$V = \frac{\pi \times d_m^2}{4} \times L,$$

where L and d_m^2 are the length and median diameter of the growth unit, and π is equal to 3.1416. An epicormic branch was considered above the reduction pruning cut when epicormic branch initiation or growth reached beyond the height of the reduction pruning cut. To be considered a problematic epicormic branch, part of the growth unit had to be in contact with the virtual wire corridor zone located 5.5 m above the ground. The mean number, volume, and tallest epicormic branch per reduction pruning treatment were obtained by averaging the number, sum, and length results of each tree, whereas mean height was obtained by averaging epicormic branches height per tree prior averaging per reduction pruning treatment.

1.3.3.2 Reduction pruning and wound closure rate

Immediately after reduction pruning of the main stem in 2015 and at the end of the growing season in 2016 and 2017, the vertical length (parallel to the retained scaffold branch of the main stem reduction pruning) and horizontal width of the pruning wound, both crossing the pith, were measured with a caliper to the nearest centimeter to determine the rate of pruning-wound closure. Each year, the surface area of the wound (S) not fully closed by the callus tissue was calculated as an ellipse according to the formula:

$$S = \frac{(L \times l) \times \pi}{4},$$

where L and l are vertical length and horizontal width respectively. The pruning wound closure rate was expressed as a percentage of the immediate surface wound area after pruning reduction.

1.3.3.3 Discolored wood area following reduction pruning

At the time of harvest in 2017, a 1-m trunk section containing wound-reduction pruning treatments and two 0.5-m trunk sections containing both selected aspect ratios of controls were removed from trees with a chainsaw. Lateral branches originating within these sections were removed close to the union with the trunk, with the exception of the retained scaffold branch of the main stem reduction pruning, where a length of 5 cm was preserved. All trunk sections were dissected with a sliding table saw along a radial longitudinal plane of 30 cm, bisecting both centers of the reduction pruning wound and the scaffold branch. Dissected sections were progressively polished with up to 400-grit sandpaper and scanned at 2400 dpi. The area of discolored wood on each scan was delineated, and its surface area was calculated based on pixel counts using Adobe Photoshop CC 2018 (Adobe Systems, Inc., San Jose, CA, USA). All areas of discoloration were normalized by dividing by the length of cross-sectional pruning cut

area. The final area of discolored wood per reduction pruning wound was computed as the average of the two halves.

1.3.4 Statistical analysis

Linear mixed effect models were used to predict epicormic branch (height, number, volume, tallest, and problematic) and wound (closure rate and discolored area) responses as a function of reduction pruning intensity and season. Sampling blocks were included in the models as a random effect. Differences between cultivars were first tested, and because they were found similar (Figure 1.S1), models were rerun with both cultivars pooled. As no interaction between reduction pruning intensity and season was found in any model, these results are not presented. To examine the effects of reduction pruning treatment over time on the density and volume of epicormic branches in the 2015, 2016, and 2017 cohorts, a multivariate analysis of variance (MANOVA) was performed. Main effects were treatments and years. All statistical analyses were conducted using JMP software, version 13.0.0 (SAS Institute, Cary, NC, USA).

1.4 Results

1.4.1 Physiological tree response after reduction pruning treatments

In 2017, two years after reduction of the main stem, the dynamics of epicormic branch initiation and development through treatments above the pruning cut were similar to the epicormic branches dynamics of the whole tree (Figure 1.1). All reduction pruning treatments had greater effects on the epicormic branch initiation and development than control trees (Figure 1.1; results not shown). For all season treatments, a higher intensity of reduction pruning of the main stem significantly increased the number ($F_{1,7} = 106.71$, $p < 0.0001$), height ($F_{1,7} = 8.74$, $p = 0.0212$), and volume ($F_{1,7} = 70.19$,

$p = 0.0002$) of epicormic branches located above the pruning cut. The pruning season had no effect on the number ($F_{2,14} = 1.69$, $p = 0.2195$) or height of epicormic branches ($F_{2,14} = 0.82$, $p = 0.4612$) for any intensity of reduction pruning treatment; however, reduction pruning during winter increased epicormic branch volume ($F_{2,14} = 4.73$, $p = 0.0270$) and the height of the tallest epicormic branch ($F_{2,14} = 8.3$, $p = 0.0042$) at the end of the second growing season.

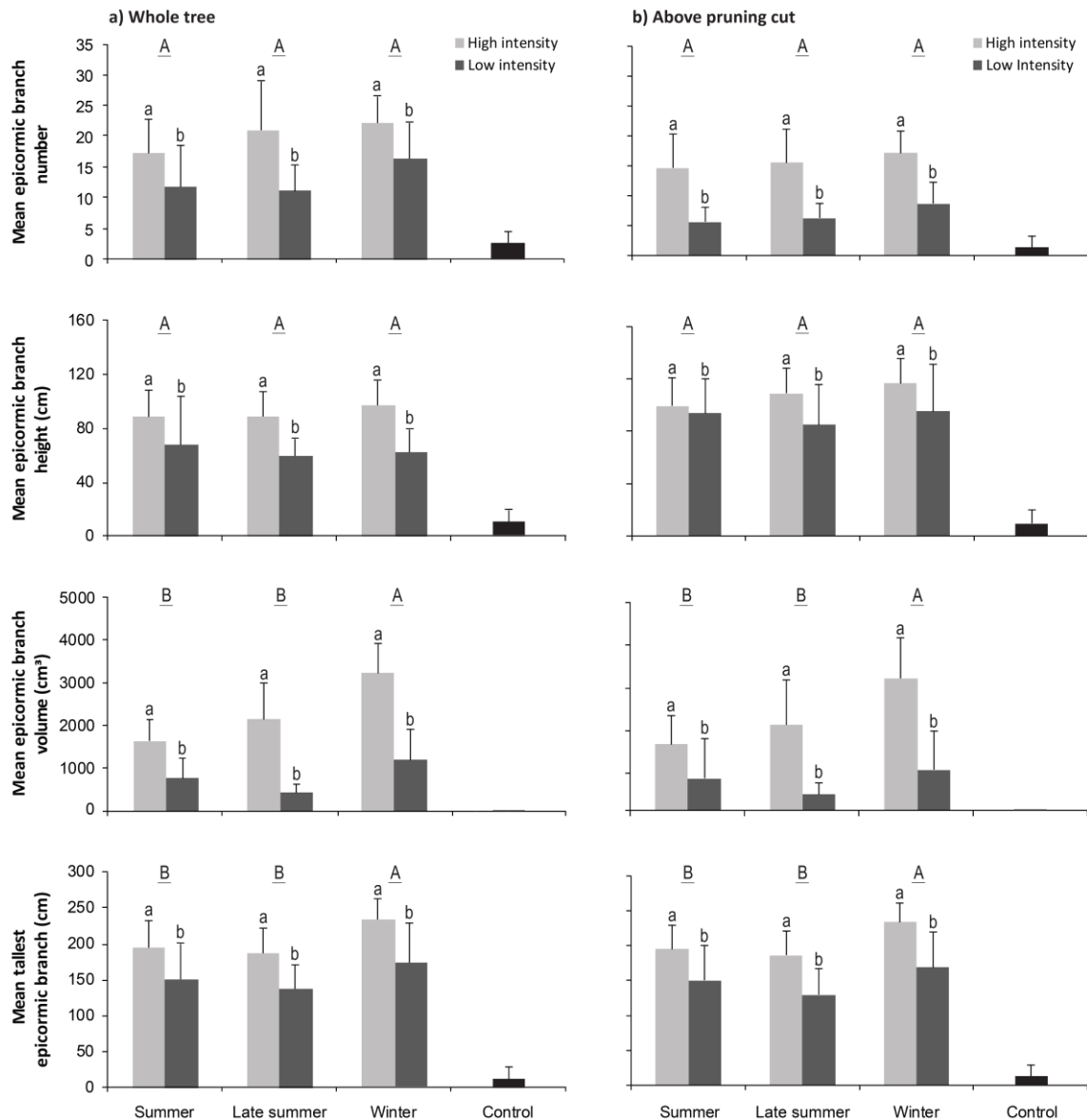


Figure 1.1 Mean (\pm SD) number, height, volume, and tallest epicormic branch after reduction of the main stem and two growing seasons by pruning intensity and by season: (a) on the whole tree (left panel) and (b) above the pruning cut (right panel). Differences between intensities within seasons: different letters above the bars indicate significant differences based on paired t-tests. Differences between seasons within intensities: capital letters above the bar pairs indicate significant differences based on Tukey's HSD post hoc tests ($p > 0.05$). Controls have been excluded from analyses, controls are shown in the graph.

1.4.2 Epicormic branch cohort establishment and survival dynamics

Between 2015 and 2017, total epicormic branch density above to the reduction pruning cut varied over time, reaching a maximum in 2017, i.e., two years after reduction of the main stem (Figure 1.2; MANOVA, $F_{2,41} = 162.95$, $p < 0.0001$). The 2015 epicormic branch cohort was influenced by treatments of pruning intensities and seasons (MANOVA, $F_{5,42} = 6.55$, $p < 0.0001$) but not by years (MANOVA, $F_{2,41} = 2.97$, $p = 0.0623$) or the interaction between treatments and years (MANOVA, $F_{10,84} = 1.56$, $p = 0.1326$). Subsequent univariate ANOVAs and Tukey HSD post-hoc tests indicated that in 2016 and 2017, one and two years after reduction pruning of the main stem, the 2015 cohort was significantly denser in response to a higher summer pruning intensity compared to the lower summer pruning intensity and all other treatments. The 2016 epicormic branch cohort was also influenced by treatments of pruning intensities and seasons (MANOVA, $F_{5,42} = 11.56$, $p < 0.0001$) and by years (MANOVA, $F_{1,41} = 5.93$, $p = 0.0192$), but not by the interaction between treatments and years (MANOVA, $F_{4,42} = 0.66$, $p = 0.6524$). In 2016, the epicormic branch cohort was significantly denser in response to the higher intensity of reduction pruning treatments compared to the lower intensity of reduction pruning treatments, except for epicormic branch density during the high-intensity summer treatment, which had an intermediate density between that of late summer and winter with the high intensity treatment and other treatments with the low intensity treatment (univariate ANOVAs and Tukey HSD post hoc tests). In 2017, the density of the 2016 epicormic branch cohort in all reduction pruning treatments was only slightly different than in 2016 (late summer and winter with high intensity > all other treatments). In 2017, the contribution of the 2016 epicormic branch cohort to the total density of epicormic branches was maximized in both the late summer and winter reduction pruning treatments. The 2016 cohort compensated for the cohort initiated in 2015 in all summer reduction pruning treatments, and total density by intensity reached similar levels compared to all seasons from 2016 onwards. The contribution of the 2017 cohort to the total density of the epicormic branches in all treatments, two years after

reduction pruning, was minimal and no significant differences in absolute density occurred among seasons and intensities (Figure 1.2; univariate ANOVAs and Tukey's honestly significant difference (HSD) post-hoc tests).

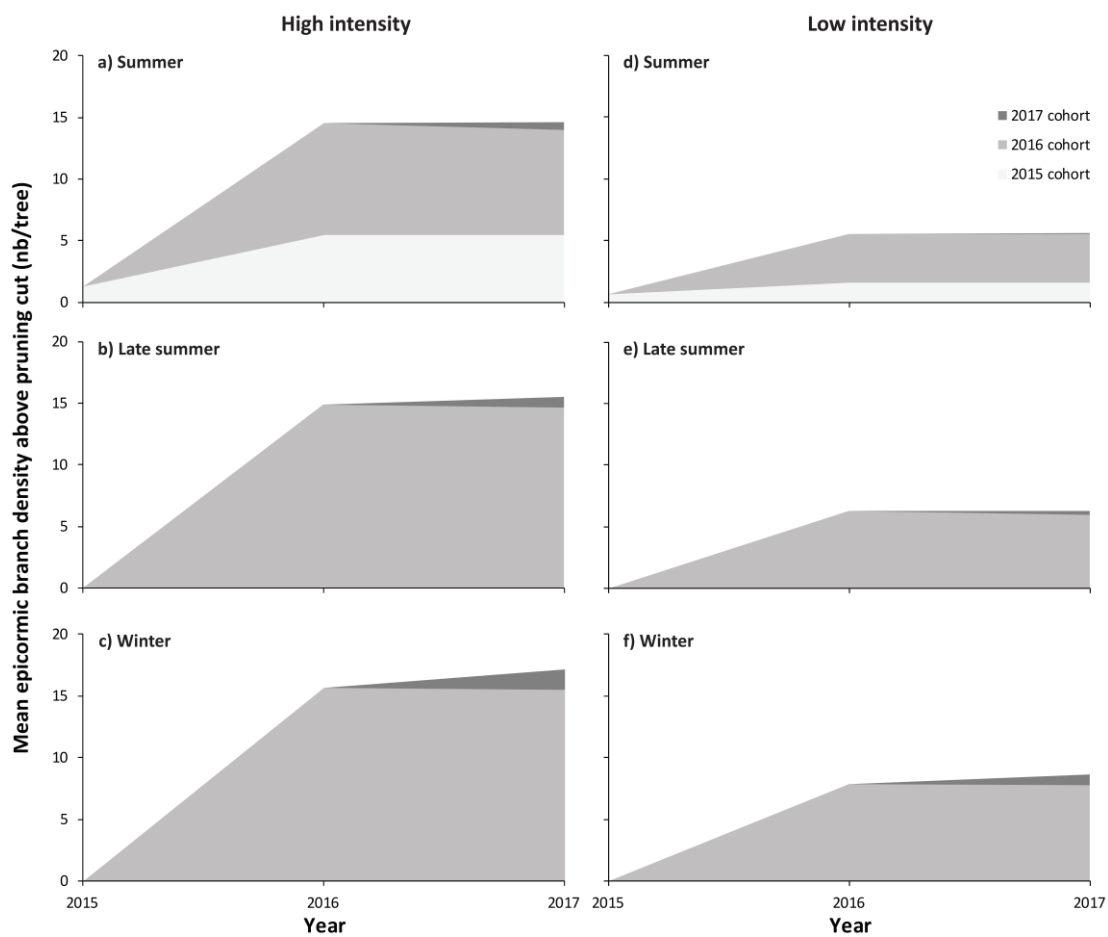


Figure 1.2 Temporal dynamics of epicormic branch densities after reduction of the main stem and above the pruning cut by cohort and by year for each of the pruning intensities and seasons. Legend for high -intensity pruning (left panel) is the same as that for low-intensity pruning (right panel).

1.4.3 Epicormic branch volume cohort and recovery dynamics

Following the main-stem reduction in 2015, total epicormic branch volume above to the reduction pruning cut increased over time (Figure 1.3; MANOVA, $F_{2,41} = 86.27$, $p < 0.0001$). The volume of the 2015 epicormic branch cohort was influenced by treatments of pruning intensities and seasons (MANOVA, $F_{5,42} = 3.77$, $p = 0.0065$), years (MANOVA, $F_{2,41} = 5.12$, $p = 0.0103$), and the interaction between treatments and years (MANOVA, $F_{10,84} = 3.09$, $p = 0.0021$). In 2016 and 2017, one and two years after reduction pruning of the main stem, the 2015 cohort contributed to the total epicormic branch volume in both summer treatments but was absent in late summer and winter treatments (univariate ANOVAs and Tukey's HSD post hoc tests). The volume of the 2016 epicormic branch cohort was also influenced by treatments of pruning intensities and seasons (MANOVA, $F_{5,42} = 17.29$, $p < 0.0001$), years (MANOVA, $F_{1,42} = 112.68$, $p < 0.0001$), and the interaction between treatments and years (MANOVA, $F_{5,42} = 16.34$, $p < 0.0001$). Subsequent univariate ANOVAs and Tukey's HSD post-hoc tests indicated that, in 2016 and 2017, the volume of the 2016 cohort was more significant during winter with high intensity of reduction pruning compared with all other reduction pruning treatments. However, the volume of the 2016 cohort with low intensity of reduction pruning was the lowest in both summer and late summer, whereas volume was intermediate in late-summer with the high-intensity of reduction pruning treatment and in the winter with the low-intensity of reduction pruning treatment. The only exception being with the low-intensity reduction pruning treatment in the 2016 where epicormic branch volume was no different than that of reduction pruning treatments with the lowest volume. In 2017, the contribution of the 2016 epicormic branch cohort to the total epicormic branch volume was maximal in both the late summer and winter reduction pruning treatments, whereas in all summer reduction pruning treatments, the volume of the 2016 cohort was only marginally different from the volume of the 2015 cohort. The contribution of the 2017 cohort to the total epicormic branch volume in all treatments two years after reduction pruning

of the main stem was minimal, and no significant differences in absolute volume occurred among seasons and intensities (Figure 1.3; univariate ANOVAs and Tukey's HSD post-hoc tests).

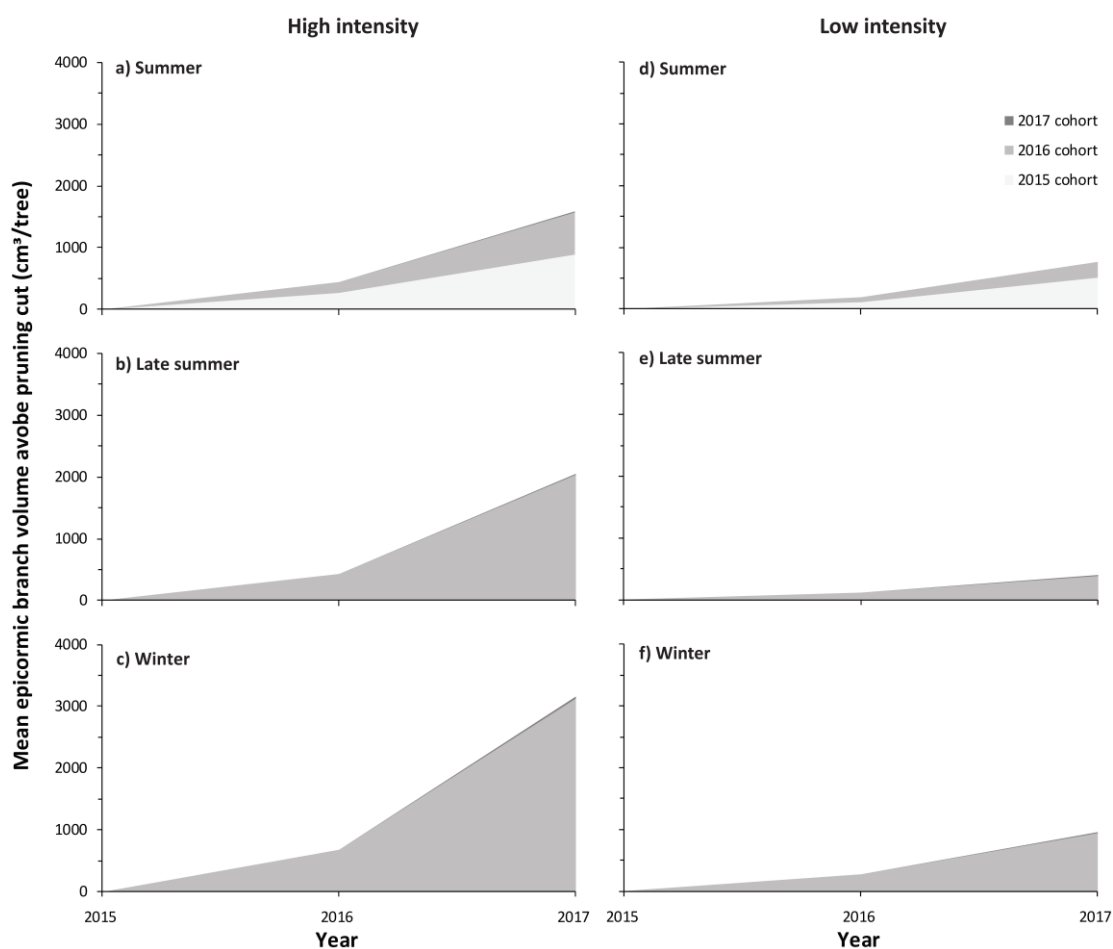


Figure 1.3 Temporal dynamics of epicormic branch volumes after reduction of the main stem and above the pruning cut by cohort and year for each of the pruning intensities and seasons. Legend for high -intensity pruning (left panel) are the same as that for low-intensity pruning (right panel).

1.4.4 Power line clearance standards and reduction pruning treatments

Two years after the main-stem reduction, in all season treatments, the number of problematic epicormic branches in contact with the virtual 2.5-m wire corridor zone was significantly higher in the lower intensity of reduction pruning treatments compared with higher intensity (Figure 1.4; $F_{1,7} = 12.44$, $p = 0.0096$). By contrast, no significant difference in the volume of problematic epicormic branches existed between intensity treatments (Figure 1.4; $F_{1,7} = 0.05$, $p = 0.8288$). At both intensities, reduction pruning during winter increased the number ($F_{2,14} = 4.04$, $p = 0.0412$) and volume ($F_{2,14} = 9.23$, $p = 0.0028$) of problematic epicormic branches compared with other reduction pruning seasons, except that the number of epicormic branches during summer reduction pruning had intermediate values between the late-summer and winter treatments.

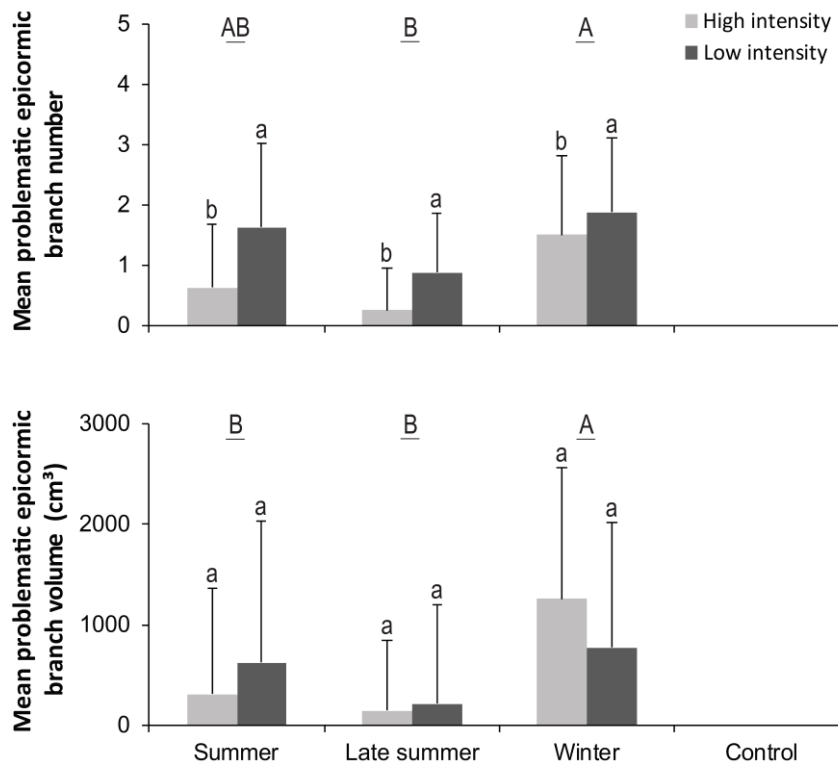


Figure 1.4 Mean (\pm SD) number and volume of problematic epicormic branches in contact with the corridor zone of a wire located 7 m above the ground after reduction of the main stem and 2 growing seasons by pruning intensity and by season. Differences between intensities within seasons: different letters above the bars indicate significant differences based on paired t-tests. Differences between seasons within intensities: capital letters above the bar pairs indicate significant differences based on Tukey's HSD post hoc tests ($p > 0.05$). Note that there is no letter for controls because epicormic branch absence has not been included in the statistical general linear model.

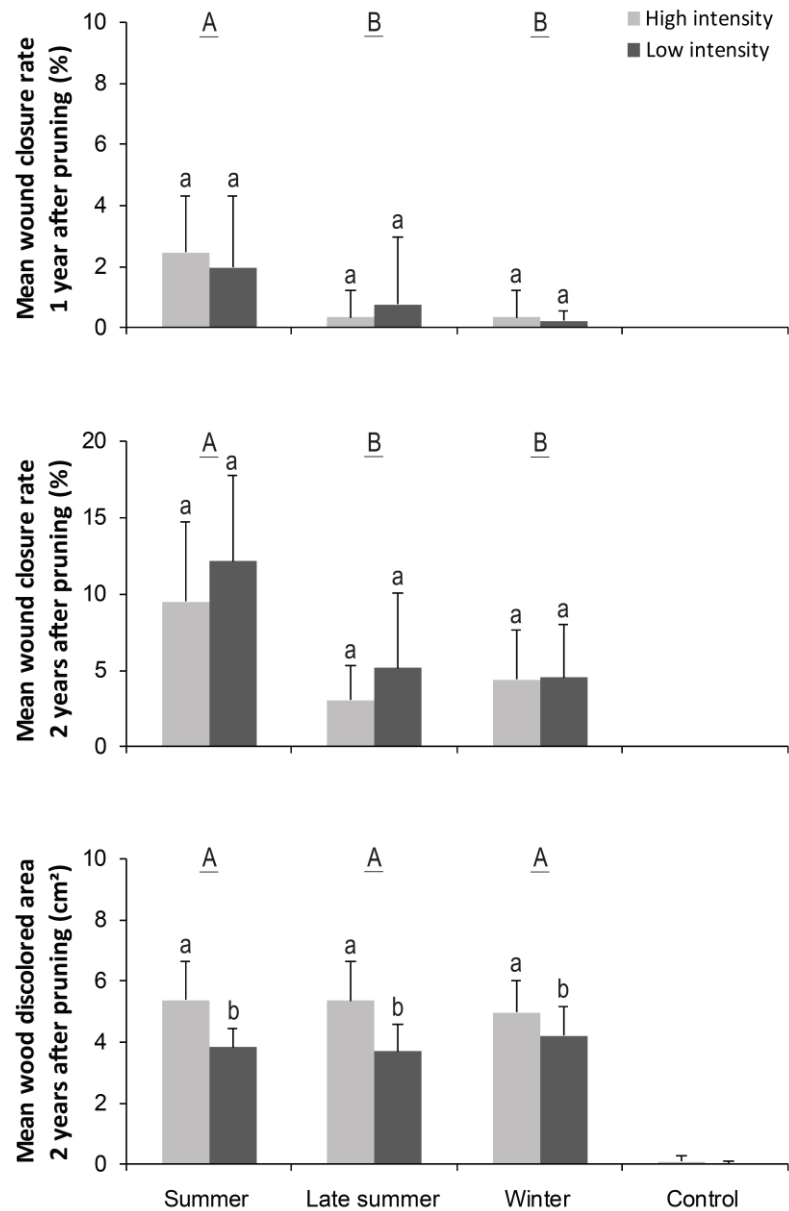


Figure 1.5 Mean (\pm SD) wound closure rate one and two years after reduction pruning, and the area of discolored wood two years after pruning reduction by pruning intensity and by season. Differences between intensities within seasons: different letters above the bars indicate significant differences based on paired t-tests. Differences between seasons within intensities: capital letters above the bar pairs indicate significant differences based on Tukey's HSD post hoc tests ($p > 0.05$). Note that for controls there is no bar for wound-closure rate because no data were collected, and there is no letter for the area of discolored wood because data have not been included in the statistical general linear model.

1.4.5 Reduction pruning treatment and wound compartmentalization

In 2016 and 2017, one and two years after reduction pruning of the main stem, the pruning wound-closure rate followed the same significant pattern among treatments (Figure 1.5). The closure rate was similar between intensities (2016, $F_{1,7} = 0.01$, $p = 0.9091$; 2017, $F_{1,7} = 1.80$, $p = 0.2210$) but was higher when reduction pruning was performed during the summer (2016, $F_{2,14} = 7.00$, $p = 0.0078$; 2017, $F_{2,14} = 14.44$, $p = 0.0004$).

Conversely, the discolored area of the wound was significantly higher with higher pruning intensity after two growing seasons ($F_{1,7} = 51.98$, $p = 0.0002$), but was not influenced by pruning season ($F_{2,14} = 0.03$, $p = 0.9717$).

1.5 Discussion and Conclusions

1.5.1 Intensity and timing of reduction pruning on epicormic branch development

The results from our study show that trees can vigorously respond by epicormic branches after a main-stem reduction pruning (Figure 1.1). The fact that a higher pruning reduction intensity resulted in an increased number and volume of epicormic branches, and that the resulting epicormic branches were taller than those produced after lower-intensity pruning reductions, confirmed that reduction pruning intensity largely controls the epicormic branches response. However, the intensity was not the sole factor controlling the emergence of epicormic branches, as epicormic branches were also present in control trees. Colin et al. (2010) previously reported that epicormic branches can occur with an increase in light availability after stand thinning. This could explain the production of epicormic branches in our control trees after reduction of the main stem of adjacent trees. Still, the lack of, or very low, epicormic branching found on control trees compared with those in other reduction pruning treatments indicates

that reduction pruning intensity was a major driver of the epicormic branches response. Although intensity has been reported as the primary factor causing epicormic branching with total removal of the main stem following harvesting (Kays and Canham, 1991; Babeux and Mauffette, 1994) or primary branch order following pruning (O'Hara et al., 2008; DesRochers et al., 2015), this is the first study to our knowledge linking pruning intensity to epicormic branches response when only the main stem of the tree is reduced. Therefore, our study provides key knowledge related to our overall understanding of the physiological response of the main stem with reduction pruning. However, to achieve a global perspective of the understanding of the physiological tree response to reduction pruning, a similar study should be undertaken at the branch scale.

The timing of main-stem reduction pruning during the year, corresponding to the leaf-on or leaf-off period, is a significant factor in the development of epicormic branches, although to a lesser extent than reduction pruning intensity (Figure 1.1). O'Hara et al. (2008) and DesRochers et al. (2015) previously demonstrated this with the removal of lower primary branch order of the living crown for silvicultural purposes. However, because winter pruning was performed before summer pruning in those studies, a delay equivalent to half a growing season for the initiation and development of the epicormic branch arose on trees pruned in summer, which could have significantly impacted the results (O'Hara et al., 2008). In our study, summer reduction pruning was applied before winter reduction pruning, and despite a decrease of density and mean height of epicormic branches on trees pruned in summer compared with those pruned in winter, the differences were not large enough to be statistically significant. Nonetheless, because at the end of the 2017 growing season, summer-pruned trees have more than half of a growing season compared to winter-pruned trees to restore the energy balance between the above- and below-ground systems, it appears safe to presume that summer or late-summer reduction pruning should result in epicormic branch densities and heights less than those obtained with winter reduction pruning, especially because the volume and the tallest epicormic branch were lower on trees pruned in the summer (Figure 1.1).

These last results corroborate previous findings by Kays and Canham (1991), and Perrette et al. (2014) on deciduous broadleaved trees, three years after total main-stem harvesting. According to Kays and Canham (1991), divergence in epicormic branches development between seasons is related to a phenological gradient in carbohydrate reserves. In fact, pruning during the leaf-on season, when stored reserves are low (Barbaroux and Bréda, 2002; Furze et al., 2018), limits the potential for epicormic branches development. Conversely, epicormic branches development is higher when pruning occurs during the leaf-off season, when stored reserves are highest.

1.5.2 Epicormic branch cohort recovery dynamics

By examining individual epicormic branch cohorts generated after applying reduction pruning to the main stem, our study was able to show contrasting dynamics of density and volume over time (Figures 1.2 and 1.3). The first epicormic branch cohort was immediately initiated in the second half of the year of growth following both main-stem reduction intensities in the summer (Figure 1.2a and d). However, the initiation of a new cohort in the second growing season of summer reduction pruning that was more dense than the first one showed that the contribution of the first cohort was not enough to restore the energy balance between the above- and below-ground systems. Nevertheless, because the volume of the first cohort at the end of the third growing season was higher than the volume of the second cohort at both reduction pruning intensities, this finding emphasizes the predominance of the first cohort initiated in the process of recovery on a tree pruned in summer (Figure 1.3a and d). A similar finding was observed with both late-summer and winter reduction pruning intensities after the two growing seasons, as epicormic branch density and volume were primarily composed of the cohort initiated during the first growing season (Figures 1.2-3b, c, e, and f). On one hand, this result suggests an incapacity of trees pruned in late summer to instantly initiate the restoration process in the year of pruning. This could be related

to the short length of the remaining growing season (Figures 1.2-3b and e). On the other hand, this once again highlights the dynamics and primary role of carbohydrate storage levels for epicormic branch development as a lower volume of epicormic branches with a similar density were produced in late summer compared with winter reduction pruning at the end of both growing seasons (Figure 1.3b, c, e, and f). Considering that reduction pruning in late summer was performed at the time of maximal carbohydrate storage (Furze et al., 2018), late-summer pruning appears to have circumvented the buildup of carbohydrates for optimal epicormic branch development in the following growing season.

The minor establishment of a third cohort in the summer reduction pruning treatment and a second cohort in both the late-summer and winter reduction pruning treatments indicates that the entire system was equilibrated after one and a half growing seasons for summer and only one growing season for late-summer and winter reduction pruning (Figure 1.2). Thus, the epicormic branches density dynamics in the time after reduction of the main stem and between the leaf-on and leaf-off periods are in agreement with previous studies, such as Perrette et al. (2014) following total harvesting, and DesRochers et al. (2015) after crown-raising of the main stem. This indicates that the epicormic branches dynamics initiated to rebuild the loss of leaf area is independent from the intensity of the operations completed on different parts of the tree.

1.5.3 Line clearance and problematic epicormic branches

Our study examined the number and volume of epicormic branches that should be removed in according to clearance standards two years after reduction pruning of the main stem. Unexpectedly, a lower pruning intensity increased the number of problematic epicormic branches when compared with the higher pruning intensity (Figure 1.4). Several authors reported that removing less than 30% (Collier and

Trumblon, 2001; O'Hara et al., 2008; Maurin and DesRochers, 2013) or 20% (Grabosky and Gilman, 2007; Dujesiefken et al., 2016) of the biomass limited epicormic branch development. In our study, a low pruning intensity removed 35 to 52% of the biomass because the trees were in contact with a virtual power distribution network located 7 m above the ground. As a result, the low-intensity reduction pruning was performed between 3 and 3.5 m above the ground and problematic epicormic branches appeared two years later. Our results therefore suggest that this reduction pruning was high because it was carried out too late in tree development. From a management point of view, if the aim is to intervene less by reducing epicormic branch development, the reduction pruning intervention should be performed before trees reach anywhere from 4.5-5.5 m tall in the case of moderately high wires (<7-8 m). In other words, trees should be reduced and shaped when younger and not yet in contact with wires. If not, reduction pruning intensity has to be increased, thus intensifying epicormic branch development (Millet and Bouchard, 2003). In addition, intervening during the leaf-on season, and especially in late-summer, (mid-August to September) before leaf fall, should result in the development of fewer problematic epicormic branches (Figure 1.4).

1.5.4 Intensity and timing of reduction pruning on wound compartmentalization

All pruning reduction treatments were followed by an active establishment of wound compartmentalization at the reduction cutting point (Figure 1.5). Smaller pruning wounds have been extensively reported as occluding faster than bigger ones at least five years after pruning (Nicolescu et al., 2013; Dănescu et al., 2015; Sheppard et al., 2016). In our study, the wound closure rate was similar between low- and high-intensity pruning after the first growing season. Although not significant, the wound closure rate became more important with a lower pruning intensity at the end of the second growing season (Figure 1.5). This lack of a significant result may be associated with the fact

that some wound diameters at the low pruning intensity were larger than those at the high pruning intensity or because wound diameter in our study was nearly twice that reported in previous studies. This suggests that only two growing seasons after pruning was an insufficient length of time for a significant difference of wound-closure rate on bigger wounds to be revealed. However, the positive impact of low-intensity of reduction pruning on wound compartmentalization at the cutting point was the proportion of the discolored wood area produced, which was significantly less than the area of discoloration resulting from the high-intensity of reduction pruning treatment (Figure 1.5). This result highlights the importance of reducing the main stem (i.e. the diameter of the cut) as little as possible to limit large pruning wounds, thus lowering risk of decay (Dujesiefken and Stobbe, 2002; Ow et al., 2013; Dănescu et al., 2015).

In relation to lowering or preventing decay, the season of pruning may also affect the efficiency of wound compartmentalization (Figure 1.5). Thus, with only half of an additional growing season, the wound closure rate of summer reduction pruning was two-fold higher than that with late summer and winter reduction pruning in both years following pruning. Numerous studies on several species have shown similar responses between season of cambial activity and dormancy (Dujesiefken et al., 2005a; Lee and Lee, 2010; Dănescu et al., 2015). Nonetheless, the fact that wound occlusion of trees that underwent late summer and winter reduction pruning was comparable indicates that trees pruned in late summer fail to instantly initiate the wound recovery processes in the year of pruning, probably because the meristem activity is already in its dormancy mode or in preparation (Meier et al., 2012), whereas this process of recovery was noticeable around the wounds of trees pruned during the summer. However, our study was unable to provide a clear consensus on the optimal season to prune to reduce the proportion of the discolored wood area produced at the cutting point (Figure 1.5). Some summer pruning wounds had large discolored wood areas that were associated with a different color and were not observed in smaller wounds, suggesting that in some cases pruning in summer may have hastened the spread of fungal infection (Chou and

MacKenzie, 1988). Still, a significant result between season and closure rate of wound were found, suggesting that summer pruning may promote faster recovery by limiting the entry time for invading microorganisms and oxygen on exposed wounds, and may limit discoloration and decay expansion after several years (Boddy and Rayner, 1983; Pearce, 1991; Schwarze and Fink, 1997), especially because winter pruning could enhance cambial dieback (Dujesiefken et al., 2005b; Lee and Lee, 2010) and promote cracks near the wound edges (Gilman, 2011).

1.6 Management Implications

The establishment and development of epicormic branches after reduction of the tree main stem follows similar trends from other silvicultural practices regarding the intensity and timing of the operation. Greater pruning intensities produced a greater number, length, and biomass of epicormic branches as well as lower compartmentalization of the pruning wound, which highlights the importance of reducing the main stem as little as possible to prevent the occurrence of epicormic branches and decay. This study also showed that if a reduction of the main stem is required to encourage the occurrence and establishment of scaffold limbs at a safe distance from wires running 7 m above the ground, it would be preferable to perform this intervention before the tree main stem has reached the wire, and specifically before or soon after it reaches the security corridor zone (Figure 1.6). Otherwise, even when using a lower reduction pruning intensity, this intensity will remove more than 30% of the biomass in line with wire clearance standards, which can trigger problematic epicormic branch development. Thus, depending on the wire height and the minimum clearance height needed for urban infrastructure, reduction of the main stem should be undertaken during the first phase of the tree-training pruning schedule to limit the need for a stronger reduction pruning intensity later on (Dujesiefken et al., 2016). We suggest that the better approach would be to intervene less severely ($\leq 20\%$ of biomass

removed at each pruning cycle) but more often (every two years) during the first 15 years following planting in order to train trees under the electrical distribution network before they reach maturity, as described by Dujesiefken et al. (2016) for ornamental trees. Such an approach should help to lengthen the maintenance return interval when trees will reach mature phases (McPherson et al., 2005; Dujesiefken et al., 2016).

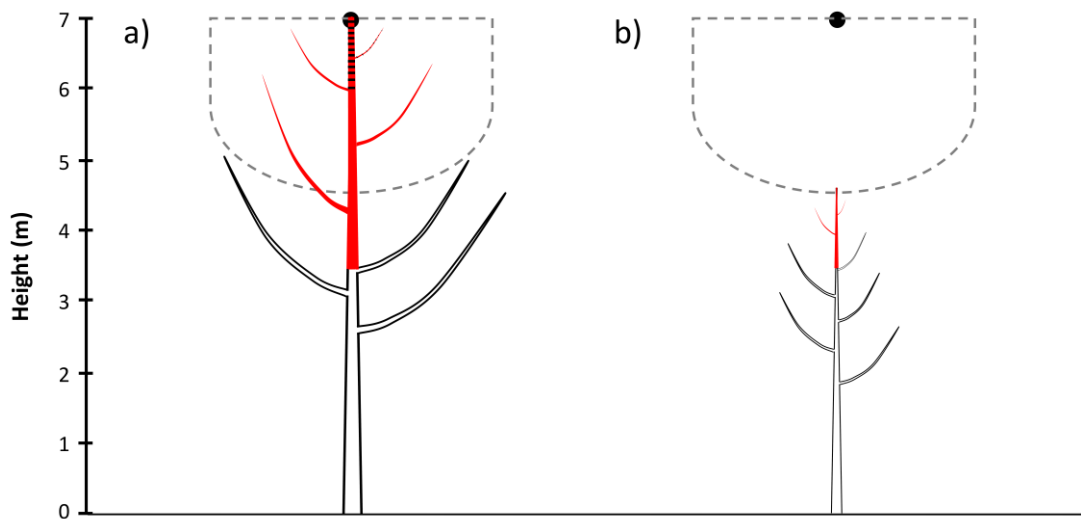


Figure 1.6 Illustration of reduction of the main tree stem for a wire running 7 m above the ground (black filled circle) and the security corridor (dashed grey line). The red part indicates the biomass that needs to be removed in line with clearance standards and for the implantation of scaffold limbs at a safe distance with the wire. (a) The main-stem reduction pruning will remove more than 30% of the biomass because the main stem is in contact with the wire, which will exacerbate epicormic branches and reduce compartmentalization at the point of cutting. The black dashed lines represent an appropriate main-stem reduction-pruning dose for a 7-m tree. (b) Reduction pruning of the main stem before a tree reaches the security corridor, which will remove less than 30% of the biomass (ideally $\leq 20\%$), decreases epicormic branches and improves compartmentalization at the point of cutting.

Reduction pruning during the leaf-on season can also limit the occurrence and development of epicormic branches compared with reduction pruning during the leaf-off season. Summer reduction pruning with half a growing season more than winter reduction pruning to restore the energy balance between the above- and below-ground

systems reduced the biomass, number of epicormic branches, and tallest epicormic branch by 54, 33, and 15%, respectively, in contact with the corridor of the wire without further affecting the wound closure rate or the area of discolored wood at the cutting point. Therefore, tree-training under electrical distribution networks should be prioritized during the leaf-on season. Similarly, maintenance pruning, when trees have reached the mature phase, should be undertaken during the leaf-on season as long as the number of trees to prune allow it. However, when the number of trees is beyond the capacity for response during the leaf-on season, tree maintenance pruning operations will span over the year. In that case, the return interval of maintenance trees could be optimized by alternating the pruning season (Figure 1.7). In fact, trees pruned in the summer could be pruned at the next cycle during winter, and so on. Accordingly, because the return interval can be increased by half a growing season or half a year following a summer pruning, at least half a year could be saved over two maintenance pruning cycles. For a five-year maintenance return interval, the savings could correspond to at least 5% per year. All the more, pruning in late summer before leaf fall can also slightly affect the occurrence and development of epicormic branches in contact with the corridor of the power line compared with summer pruning, and could be used to increase the return interval further. It should be noted that pruning during leaf flush could also decrease the epicormic branch response when compared with summer pruning; however, this period should be avoided, especially in urban areas owing to bird nesting. Further economic analyses are suggested to validate this entire pruning season model.

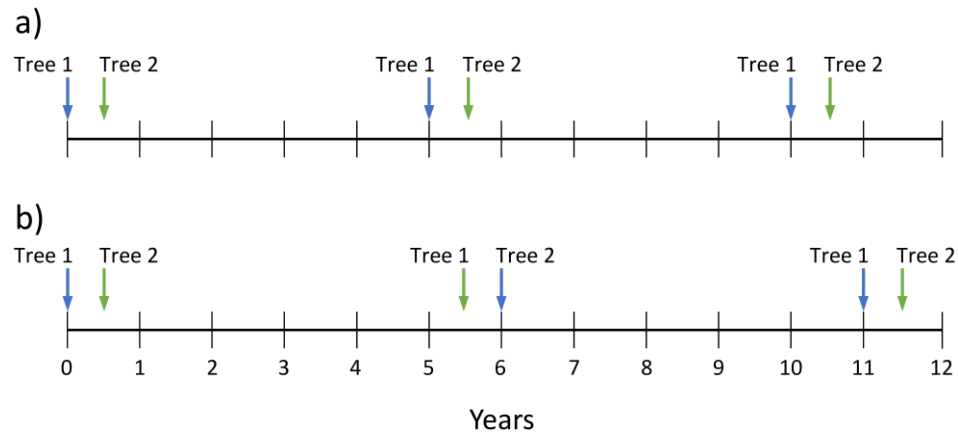


Figure 1.7 Illustration of the maintenance pruning schedule under the electricity distribution network over two pruning cycles, when trees reach the mature phase. The blue and green arrows represent winter and summer pruning, respectively. (a) Pruning cycles of five years without alternating pruning seasons between trees. (b) Alternating pruning seasons between cycles.

1.7 Acknowledgments

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1.9 Supporting information

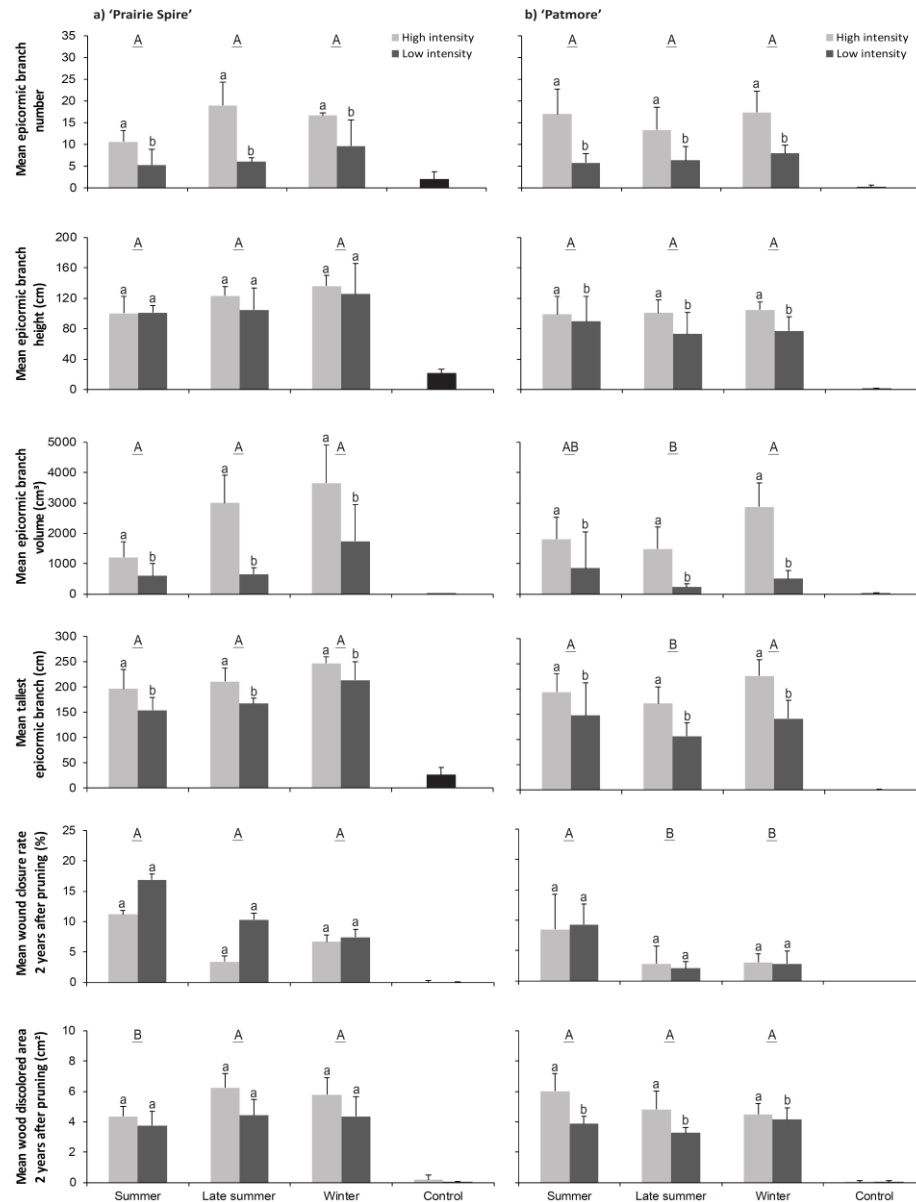


Figure 1.S1 Mean (\pm SD) number, height, volume, and tallest epicormic branch, as well as wound-closure rate and area of discolored wood two years after pruning reduction by pruning intensity and by season: (a) *Fraxinus pennsylvanica* 'Marsh'. 'Prairie Spire' (left panel) and (b) *Fraxinus pennsylvanica* 'Marsh'. 'Patmore' (right panel). Differences between intensities within seasons: different letters above the bars indicate significant differences based on paired t-tests. Differences between seasons within intensities: capital letters above the bar pairs indicate significant differences based on Tukey's HSD post-hoc tests ($p > 0.05$). Despite having been excluded from the analyses, controls are shown in the graph.

CHAPITRE II

OPTIMIZING REDUCTION PRUNING UNDER ELECTRICAL LINES: THE INFLUENCE OF TREE VIGOR BEFORE PRUNING ON TRAUMATIC RESPONSES

Perrette, G.^{1,2,4}, Delagrangé, S.^{2,4}, Ramirez, J.A.^{3,4}, Messier, C.^{1,2,4}

¹ Department of Biological Sciences, Université du Québec à Montréal, Centre Ville Station, P.O. Box 8888, Montreal, Qc, H3C 3P8, Canada

² Institute of Temperate Forest Sciences, Université du Québec en Outaouais, 58 Rue Principale, Ripon, Qc J0V 1V0, Canada

³ Facultad de Ciencias Agrarias, Universidad del Cauca, Calle 5 N° 4-70, Popayán, Colombia

⁴ Center for Forest Research, Université du Québec à Montréal, Centre-ville Station, P.O. Box 8888, Montréal, Qc, H3C 3P8, Canada

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2.1 Abstract

Reduction pruning of main tree stems is commonly performed in the maintenance of an electricity distribution network to encourage the growth of scaffold limbs away from the wires. Understanding both the epicormic branch initiation and growth after reduction pruning interventions, as well as the area of discolored wood at the cutting point are important for optimizing the pruning cycle and maintaining healthy and safe trees. In this study, we investigated post-pruning traumatic responses in relation to tree vigor before pruning in 116 hackberries (*Celtis occidentalis* L.) and 86 green ash (*Fraxinus pennsylvanica* Marsh.) growing in a semi-controlled environment of a nursery. Four years before pruning, each tree of both species was assigned a degree of damage commonly occurring in urban areas, including root injury, defoliation, and stem injury, for a total of 18 treatment combinations arranged in a randomized block design. In both species, trees that had lower vigor prior to pruning had a reduced number, height, and volume of the epicormic branches at the cutting point two years after main stem pruning. Interestingly and contrary to expectations, a positive relationship was found between the area of discolored wood at the cutting point and tree vigor prior to pruning. However, below a vigor threshold, the area of wood discoloration was exacerbated by crown mortality and retrenchment. *Celtis* showed a less efficient ability to compartmentalize and produced fewer epicormic branches compared to *Fraxinus*, and epicormic branches were of reduced height and volume when low growth was observed. Vigor of both species prior to pruning was primarily associated with root damage; however, only the traumatic responses of *Celtis* were significantly impacted from this kind of damage. From a management perspective, the results indicate that both species can survive after several damage events and after reduction of the main stem, but suggest that species with less efficient compartmentalization exhibit reduced stress-recovery resilience.

Keywords: CODIT, Pruning Return Cycle, Sucker Growth, Utility Arboriculture

2.2 Introduction

The electricity distribution network is a major city utility that requires continuous maintenance pruning of tree crowns to enhance cohabitation and ensure the safe functioning of the electrical conductor lines (Gilman, 2011; Dupras et al., 2016). When trees are planted directly under wires, reduction pruning of the main stem is commonly used during tree training to encourage the occurrence and establishment of scaffold limbs near the cutting point (Millet and Bouchard, 2003; Gilman, 2011). Afterwards, scaffold limbs are directed away from wires by directional pruning to obtain a "V" bilateral crown form (Millet and Bouchard, 2003; Gilman, 2011; Lecigne et al., 2018). However, a few years after reduction pruning interventions, the space created within the internal structure of the tree undergoes epicormic branch recolonization, which then requires repeated pruning to remove epicormic branches and maintain clearance standards (Goodfellow et al., 1987; Millet and Bouchard, 2003; Follett et al., 2016; Lecigne et al., 2018). Such repeated maintenance returns come with major expenses (Goodfellow et al., 1987; Millet, 2012) that are influenced by the period of time before return (which is governed by epicormic branch growth rates), the time needed to prune a tree (which is affected by the number of epicormic branches to remove), and the cost of biomass disposal (which is associated with the volume of epicormic branches to be chipped) (Nowak, 1990; Browning and Wiant, 1997). Consequently, to optimize maintenance of the electricity distribution network, vegetation managers have the challenge of producing good estimates of epicormic branch regrowth to schedule adequate return pruning times (Follett et al., 2016), while minimizing the pruning intensity in order to maintain healthy and safe trees for residents and infrastructure (Dujesiefken et al., 2016).

Pruning creates wounds and dysfunctional wood at the cutting point, and may provide entry for microorganisms of decay that induce cavity formation over time and alter the health, mechanical strength, and safety of the tree (Dujesiefken and Stobbe, 2002;

Dujesiefken et al., 2016). The wound compartmentalization process has been well described since the CODIT (Compartmentalization of decay in trees) model was established by Shigo and Marx (1977). Wood discoloration and the spread of decay are restricted at the cutting point by the formation of reaction zones (Gilman, 2011; Dujesiefken et al., 2016). Although numerous studies have been undertaken on the expansion of the discolored area of a wound after a branch is removed (Dujesiefken and Stobbe, 2002; Eisner et al., 2002; Gilman and Grabosky, 2006; Lee and Lee, 2010; Ow et al., 2013; Dănescu et al., 2015), we have little understanding of what happens when the main stem is reduced (Grabosky and Gilman, 2007).

In managed forests, less vigorous trees have been shown to produce more epicormic branches on the bole following a stand thinning (Nicolini et al., 2001; Colin et al., 2008) and to have a higher proportion of discolored wood (Baral et al., 2013); however, results could differ in urban areas due to differences in environmental conditions (Close et al., 1996; Dujesiefken et al., 2016) and pruning contexts (Meier et al., 2012; Dujesiefken et al., 2016).

Multiple factors, including attribute of the directional pruning (i.e., where the diameter of the retained lateral branch is at least one-third that of the removed one), the intensity and season of pruning, and species have been shown to influence epicormic branch growth rate (Goodfellow et al., 1987; Millet and Bouchard, 2003; O'Hara et al., 2008; DesRochers et al., 2015; Follett et al., 2016; Perrette et al., Chapter 1) and the area of wood discoloration (Dujesiefken and Stobbe, 2002; Dahle et al., 2006; Grabosky and Gilman, 2007; Dujesiefken et al., 2016; Perrette et al., Chapter 1). However, few studies have examined the integrated response of both epicormic branch production and wood discoloration after pruning (Perrette et al., Chapter 1) or in relation to tree vigor prior to pruning (Waring et al., 2005).

Trees growing in urban areas face severe environmental conditions (Jutras et al., 2010) and must cope with a large range of stresses, such as root trenching (Jim, 2003), defoliation (Tubby and Webber, 2010), and partial trunk girdling (Vogt and Fischer, 2014). These stresses, which occur at various intensities and alone or in combination, can affect tree vigor in terms of annual primary growth (APG; Gilbertson and Bradshaw, 1985; Hodge and Boswell, 1993) or annual secondary growth (ASG; Jacquet et al., 2014; Vitali et al., 2019). By reducing the photosynthetic surface area, pruning can lower energy reserves of the tree and the storage capacity (Gilman, 2011; Maurin and DesRochers, 2013) necessary to support traumatic responses (Tschaplinski and Blake, 1994). Thus, trees with reduced vigor related to stress damage and a reduction of the main stem could express reduced traumatic responses at the cutting point. However, the magnitude of this response could also vary depending on the nature and intensity of the stress previously applied to the roots, leaves, or trunk (Waring, 1987).

The main objective of this research was to investigate the traumatic responses of two commonly used urban species in eastern North America following a reduction of the main stem along a large range of tree vigor. To obtain this range, hackberry (*Celtis occidentalis* L.) and green ash (*Fraxinus pennsylvanica* Marsh.) species were subjected to different types of mechanical damage to the roots, leaves, and trunk for four years prior to reduction pruning. A second objective was to evaluate how different kinds and intensities of mechanical damage influence traumatic responses among tree species. To control for other confounding influences associated with urban environmental conditions, i.e., urbanized types, irradiation, surficial deposit, and de-icing salt, which could have an effect on tree growth (Jutras et al., 2010), this study was carried out in the semi-controlled environment of a nursery.

2.3 Material and methods

2.3.1 Site and experimental design

The experimental plantation was established in 2009 at the Montréal Municipal Nursery in the city of l'Assomption, Québec, Canada (45°48'N 73°25'W), located 40 km north-east of Montréal. In this area, the climate is continental and humid, with hot summers and cold winters. Between 1970 and 2000, the average annual temperature was 5.3°C and the average annual precipitation was 1018.7 mm with a mean annual snow cover of 208.9 cm (Environment Canada 2018, Assomption weather station). Soil texture in this experimental plantation site ranged from mostly clay to some loam patches.

At the time of planting in 2009, 116 hackberries (*Celtis occidentalis* L.) and 86 green ash (*Fraxinus pennsylvanica* Marsh.; hereafter referred to as *Celtis* and *Fraxinus*, respectively), two species with fast growth rates (Nowak, 2003) and a similar size, were selected among field-grown seedlings propagated in 2004 and 2003, respectively. Trees of both species were planted at 2-m intervals in two rows. Annual weed control included the application of herbicide at the base of the tree stem followed by mechanical mowing.

2.3.1.1 Stress treatments

To achieve a health gradient of trees, four years after planting the trees were randomly assigned to various combinations of stress treatments that included a gradient of root reduction (0%, 37%, and 75%), defoliation (0%, 37%, and 75%), and stem damage (0% and 50%). More details on the implementation of the field design and stress processes can be found in Ramirez (2017) and Vitali et al. (2019). Overall, the experiment consisted of 18 treatments, arranged in a completely-randomized block design with 6 blocks (replicates) for *Celtis* and 4 blocks (replicates) for *Fraxinus*, with

18 trees per block. In addition, most severe combination per block was replicated on 8 *Celtis* and 14 *Fraxinus*. Diameter of *Celtis* and *Fraxinus* trees did not differ between treatment combinations before stress treatments were applied, (see Section 2.3.1; ANOVA, $F_{17,17} = 1.20$, $p = 0.28$; $F_{17,17} = 0.65$, $p = 0.84$, respectively). All stress treatments were applied in two consecutive years in July 2012 and 2013.

2.3.1.2 Reduction pruning

In 2015, at the end of the second growing season after the last stress treatments were applied, diameter at breast height (DBH) of *Celtis* and *Fraxinus* ranged from of 2.1 to 8.0 cm and 4.9 to 9.7 cm, respectively, while height ranged from 2.8-5.5 m and 4.5-7.6 m, respectively. In mid-December 2015, main-stem reduction was performed on each tree of both species. For each reduction pruning of the main stem, only one directional pruning cut was made using a hand saw to comply with the American National Standards Institute (ANSI, 2008). Diameter of the main stem cut ranged from 1.4 to 5.8 cm for *Celtis* trees and 2.7 to 7.1 cm for *Fraxinus*. No heartwood or decay was visible on any reduction pruning cut. Because the retained lateral branch diameter relative to the parent axis diameter affects the surface area of decay after reduction pruning (Eisner et al., 2002; Gilman and Grabosky, 2006), we tried to keep aspect ratio within a small range (from 0.33 to 0.51). To obtain this range, similar branch unions on each tree, without included bark or codominant aspect, were first selected and flagged in mid-August 2015. For each of the branch unions flagged, the trunk and branch diameter were measured 10 mm above the branch bark ridge with a 2-m Lufkin tape measure and the aspect ratio was determined. The total foliage to be removed from the total live canopy was then visually estimated by two assessors. The assessors agreed on the estimated pruning dose and noted it in a field spreadsheet. The final decision encompassed both the aspect ratio and the amount of foliage to be removed across a limited range from 37% to 50%.

2.3.2 Data collection

2.3.2.1 Assessments of tree health

In this study, annual primary growth (APG) and annual secondary growth (ASG) were used as an integrated trait referring to tree vigor after the application of stress treatments but prior to reduction pruning of the main stem.

In mid-December 2015, APG was measured immediately after reduction pruning. To do so, 10 annual apical shoots, taken from the outermost branches of the removed main stem, were measured per tree and averaged. The ASG was determined by dendrochronological analysis. Circular cross-sections were collected for each tree in 2017 at a height of 1.3 m. Cross-sections were progressively polished with sandpaper (up to 400-grit) and scanned at 2400 dpi. Annual ring widths were measured on three radii per cross-section using CooRecorder 7.6 software (Cybis Elektronik and Data AB, Saltsjöbaden, Sweden). CDendro software (Cybis Elektronik and Data AB, Saltsjöbaden, Sweden) was then used to cross-date the individual series and to sum them for each tree. Ring-width data averages from 2014-2015, corresponding to the growth period between the last stress treatment and the reduction pruning, were subsequently used to determine the ASG.

2.3.2.2 Epicormic branch inventory

Live epicormic branches above the pruning cut of each tree were counted and measured during late summer in 2017 (i.e., two years after reduction pruning). Each inventoried epicormic branch was first labeled using a tapener and measured for initiation height. An epicormic branch was considered to be above the pruning cut if epicormic branch initiation or the growth unit was higher than the reduction pruning cut. As defined by Bégin and Fillion (1999), all deferred or proleptic epicormic branches were counted on

the trunk and branches, as well as all immediate or sylleptic epicormic branches on branches, if their annual growth length was greater than those of the retained lateral branch of the reduction pruning. Lengths and median diameters of all growth units of each epicormic branch (Barthelemy and Caraglio, 2007) were recorded (with a ruler and caliper) at the widest part and at a right angle to obtain an average value, measured to the nearest mm. To obtain the total height and volume of each epicormic branch, the primary order lengths of growth units and growth-unit volumes of all branch orders were added. Growth unit volume (V) was calculated according to the following formula:

$$V = \frac{\pi \times d_m^2}{4} \times L,$$

where L is the length and d_m^2 is the median diameter of the growth unit. The mean number, volume, and tallest epicormic branch per treatment were obtained by averaging the number, sum, and length results for each tree, whereas mean height was obtained by averaging epicormic branches height per tree prior averaging per stress treatment.

2.3.2.3 Area of discolored wood after reduction pruning

At the time of harvest in 2017, one 1-m trunk section containing the wound-pruning treatment was removed from the tree with a chainsaw. Lateral branches originating within these sections were removed close to the union, except for the retained lateral branch of the directional pruning cut, where a length of 1-3 cm was preserved. All trunk sections were dissected with a sliding table saw along a radial longitudinal plane of 15 cm, bisecting both the centers of the pruning wound and the retained lateral branch (Figure 2.S1). One dissected section was progressively polished with sandpaper (up to 400-grit) and scanned at 2400 dpi. The area of discolored wood on each scan was delineated and the surface area was calculated based on pixel counts using Adobe

Photoshop CC 2018 (Adobe Systems, Inc., San Jose, United States). All areas of discoloration were normalized by dividing the area by the length of the cross-sectional pruning cut area.

2.3.3 Statistical analysis

Linear mixed-effect models were used to predict APG and ASG, epicormic branch responses (height, number, volume, tallest), and the area of wood discoloration as a function of stress treatment. Block was included in the models as a random effect. To examine APG and ASG effects on epicormic branch characteristics and the area of wood discoloration, regression analyses were performed with block included as a random effect. Wilks and Brown–Forsythe tests were used to test assumptions of normality and homoscedasticity, respectively. Data were initially square-root transformed if model residuals did not meet the assumptions of normality and homoscedasticity, and then log-transformed if normality and homoscedasticity of square-root transformed model residuals were not met. Differences between APG and ASG effects on epicormic branch characteristics and the area of wood discoloration between species were predicted and based on the percentage of growth compared to the maximum growth before reduction pruning. All statistical analyses were conducted using JMP software, version 14.0.0 (SAS Institute, Cary, NC, USA).

2.4 Results

2.4.1 Tree vigor and traumatic responses after reduction pruning

The APG and ASG of both species before pruning positively influenced the traumatic responses of trees two years after reduction of the main stem (Table 2.1; Figures 2.1 and 2.2). However, the influence of ASG was stronger on the number, average height,

and volume of epicormic branches, tallest epicormic branch, and area of wood discoloration (Table 2.1). For *Celtis* trees the APG and ASG relationships (R-squared values) with the number, average height, volume, and tallest epicormic branch ranged from 0.22 to 0.33 and 0.34 to 0.39, respectively. These R-squared values were lower for *Fraxinus* trees, ranging from 0.06 to 0.11 and 0.10 to 0.14, respectively. By contrast, the APG and ASG relationships (R-squared values) with the area of wood discoloration were 0.08 and 0.13, respectively, for *Celtis* trees, and higher for *Fraxinus* trees with values of 0.33 and 0.43, respectively (Table 2.1; Figures 2.1 and 2.2).

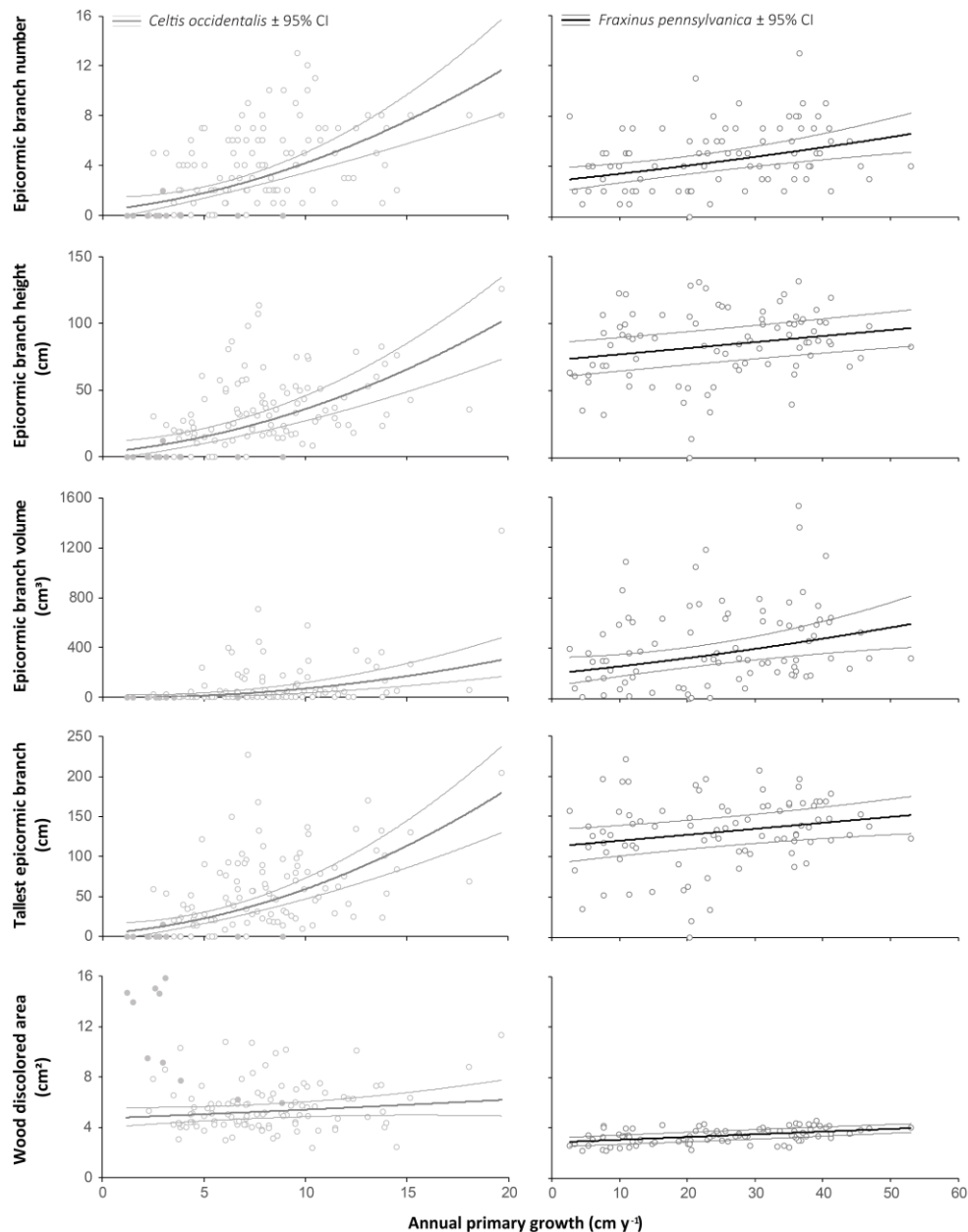


Figure 2.1 Relationships between the number, height, volume, and tallest epicormic branch as well as the area of wood discoloration two years after reduction pruning and the annual primary growth (APG) before reduction pruning of *Celtis occidentalis* (left panel) and *Fraxinus pennsylvanica* (right panel). Scales are different in the panels to maximize the visibility of the differences between species. Filled circles (left panel) represent *Celtis occidentalis* with full mortality of the retained lateral branch two years after reduction pruning. Bold lines are means of the relationships, whereas thin lines are 95% confidence intervals based on the mean. *Celtis occidentalis* shown in the graph by filled circles were excluded from analyses of the area of wood discoloration.

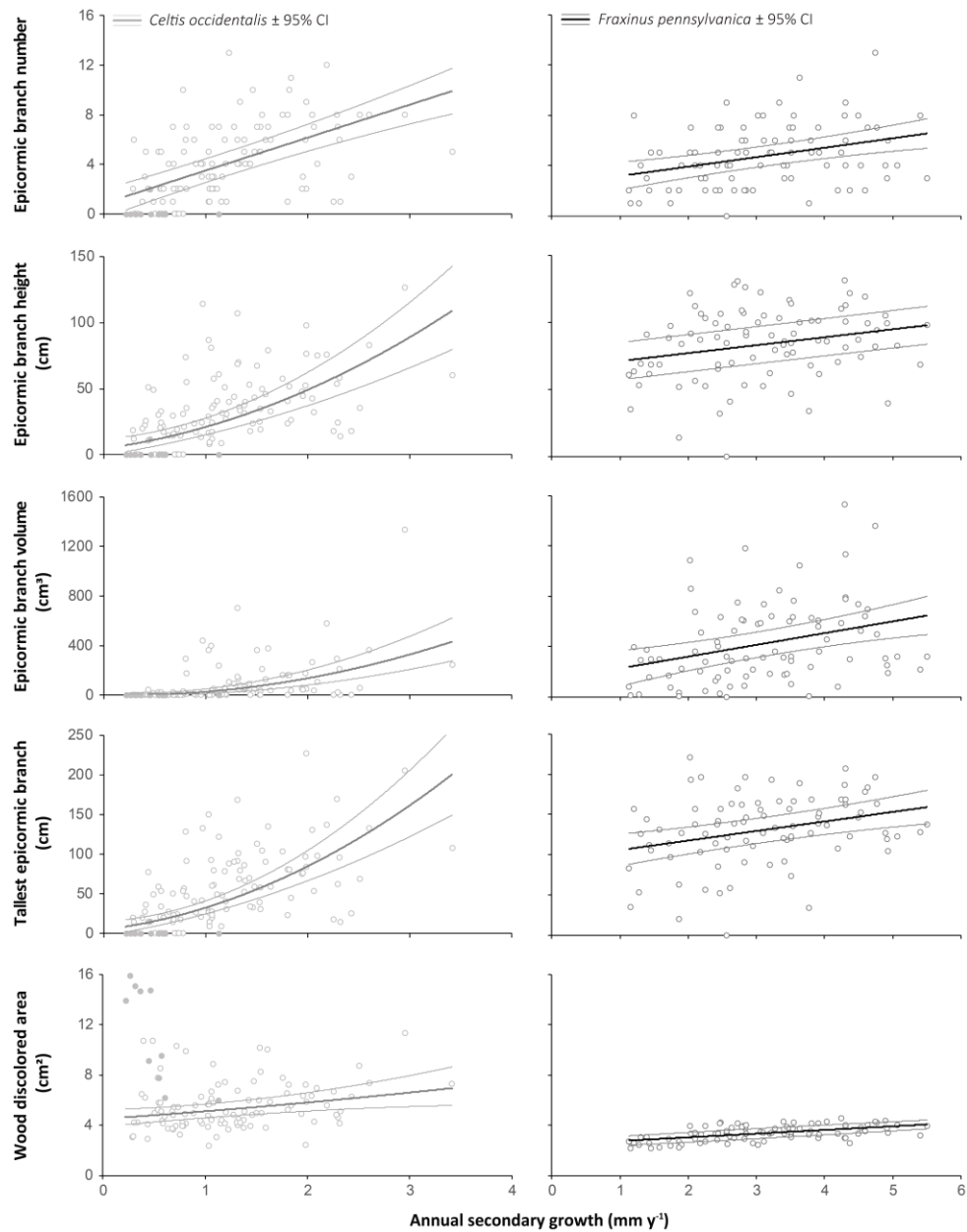


Figure 2.2 Relationships between the number, height, volume, and tallest epicormic branch as well as the area of wood discoloration two years after reduction pruning and the annual secondary growth (ASG) before reduction pruning in *Celtis occidentalis* (left panel) and *Fraxinus pennsylvanica* (right panel). Scales are different in the panels to maximize the visibility of the differences between species. Filled circles (left panel) represent *Celtis occidentalis* with full mortality of the retained lateral branch. Bold lines are means of the relationships, whereas thin lines are 95% confidence intervals based on the mean. *Celtis occidentalis* shown in the graph by filled circles were excluded from analyses of the area of wood discoloration.

Table 2.1 Regressions predicting the effects of annual primary and secondary growth (APG and ASG) before reduction pruning in 2015 on the number, height, volume, and tallest epicormic branch, as well as the area of wood discoloration in 2017 (two years after reduction pruning) of *Celtis occidentalis* and *Fraxinus pennsylvanica*.

Tested factors		Number			Height			Volume			Tallest			Wood discolored area		
		F stat	<i>p</i> -value	<i>R</i> ²	F stat	<i>p</i> -value	<i>R</i> ²	F stat	<i>p</i> -value	<i>R</i> ²	F stat	<i>p</i> -value	<i>R</i> ²	F stat	<i>p</i> -value	<i>R</i> ²
<i>Celtis occidentalis</i>	APG	36.54	0.00 *	0.22	44.09	0.00 *	0.33	23.62	0.00 *	0.23	47.87	0.00 *	0.30	2.19	0.14	0.08
	ASG	49.25	0.00 *	0.34	52.69	0.00 *	0.37	46.44	0.00 *	0.34	65.50	0.00 *	0.39	7.21	0.01 **	0.13
<i>Fraxinus pennsylvanica</i>	APG	9.96	0.00 *	0.11	3.78	0.05	0.10	7.08	0.00 *	0.06	3.65	0.06	0.08	21.91	0.00 **	0.33
	ASG	10.17	0.00 *	0.12	5.56	0.02 *	0.14	9.17	0.00 *	0.10	8.08	0.00 *	0.11	39.06	0.00 **	0.43

Statistically significant values ($P < 0.05$) are given in bold. * or ** indicate that model was square-root or log transformed, respectively.

2.4.2 Divergence in traumatic responses between species in relation to tree health

In 2017, two years after reduction of the main stem, the traumatic response dynamics through species was similar according to the APG and ASG (Figure 2.3). Based on the relative ASG (Figure 2.3), *Celtis* trees with the poorest growth before reduction pruning of the main stem produced fewer and shorter epicormic branches compared to *Fraxinus* with a similar growth (0.7 vs. 3.0; 5.1 vs. 73.6 cm; and 6.2 vs. 114.3 cm, for the number, average height and tallest epicormic branch, respectively). Conversely, *Celtis* trees with the best growth rate prior to pruning produced more and taller epicormic branches, and longer tallest epicormic branch than *Fraxinus* (11.6 vs. 6.6; 101.3 vs. 96.5 cm and 179.2 vs. 151.6 cm, for the number, average height and tallest epicormic branch, respectively). However, regardless of tree health, the epicormic branch volume of *Celtis* was lower than that of *Fraxinus* (range = 0.2-301.3 cm³ vs. 211.3-591.4 cm³, respectively). Interestingly, the area of wood discoloration at the cutting point was greater in *Celtis* compared to *Fraxinus*, regardless of tree health (range = 4.8-6.2 cm² vs. 2.9-4.0 cm², respectively).

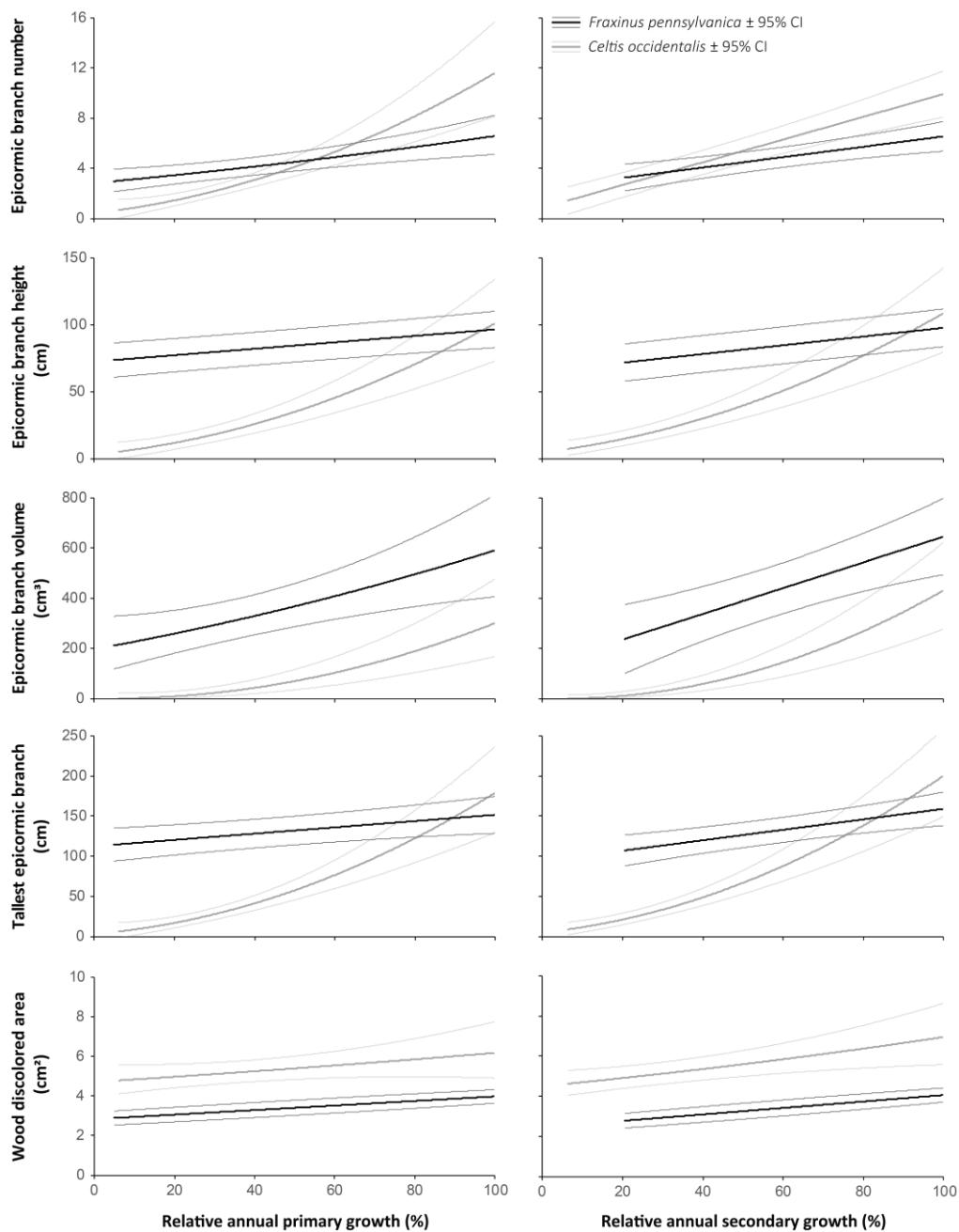


Figure 2.3 Predicted curves of the relationships between the number, height, volume, and tallest epicormic branch, as well as the area of wood discoloration two years after reduction pruning and the relative annual primary growth (APG; left panel) and secondary growth (ASG; right panel) based on the % of growth compared to the maximum growth before reduction pruning in *Celtis occidentalis* and *Fraxinus pennsylvanica*. Bold black and grey lines are means of the relationships, whereas thin black and grey lines are 95% confidence intervals based on the mean.

2.4.3 Tree vigor after stress treatments

In 2015, two years after the last stress treatment was applied and before reduction of the main tree stem, the APG and ASG of both species were found to be significantly affected by stress treatments applied to roots (Table 2.2). Tree vigor was negatively impacted by greater root reduction; however, only the treatment with 75% root removal was statistically significant, except for 37% of root removal on the APG of *Celtis*, where results were significant compared to 0% of root removal (Figure 2.4). The APG of *Celtis* was also negatively affected by defoliation and the interaction between root reduction and defoliation (Table 2.2).

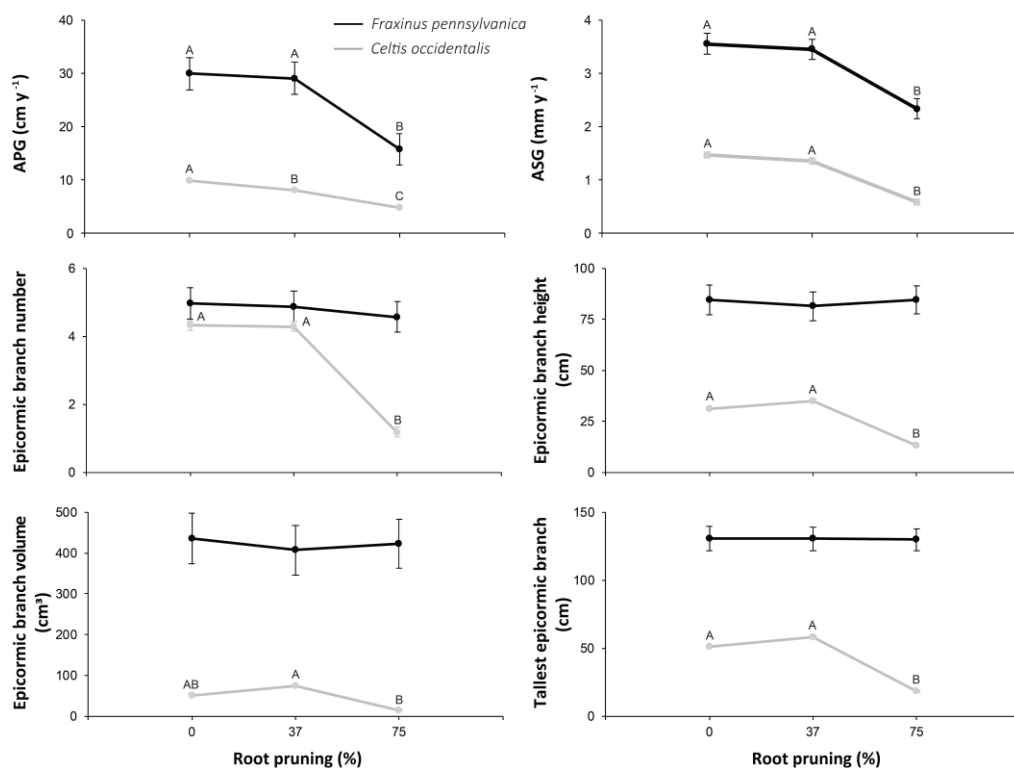


Figure 2.4 Effects of root-pruning intensity on the mean annual primary growth (APG) and secondary growth (ASG) in 2015 (two years after root treatments), and on the mean number, height, volume, and tallest epicormic branch in 2017 (two years after reduction pruning) of *Celtis occidentalis* and *Fraxinus pennsylvanica*. Error bars are standard errors of the mean. Different letters indicate significant differences based on Tukey HSD post-hoc tests ($P < 0.05$).

Table 2.2 Global linear mixed models testing the effects of root pruning (RR), defoliation (DF), stem damage (SD), and their interactions on the mean annual primary and secondary growth (APG and ASG) in 2015 (two years after treatment), and on the mean number, height, volume, and tallest epicormic branch, as well as the area of wood discoloration in 2017 (two years after reduction pruning) of *Celtis occidentalis* and *Fraxinus pennsylvanica*.

Tested factors		APG		ASG		Number		Height		Volume		Tallest		Wood discolored area	
		F stat	<i>p</i> -value	F stat	<i>p</i> -value	F stat	<i>p</i> -value	F stat	<i>p</i> -value	F stat	<i>p</i> -value	F stat	<i>p</i> -value	F stat	<i>p</i> -value
<i>Celtis occidentalis</i>	RR	105.75*	0.00	37.78*	0.00	15.26*	0.00	12.25*	0.00	6.84*	0.00	13.73*	0.00	2.68**	0.07
	DF	9.82	0.00	1.55	0.26	0.20	0.82	0.83	0.46	0.09	0.92	0.57	0.58	0.94	0.42
	SD	1.53	0.27	1.03	0.36	0.80	0.41	0.19	0.69	1.72	0.26	0.05	0.83	0.68	0.41
	RR:DF	4.09	0.01	0.86	0.50	0.21	0.93	1.46	0.25	1.05	0.41	1.12	0.38	0.18	0.95
	RR:SD	0.94	0.43	2.62	0.12	0.61	0.56	0.44	0.66	1.18	0.35	0.79	0.48	2.11	0.13
	DF:SD	0.57	0.58	0.25	0.79	0.39	0.69	1.15	0.36	1.70	0.23	1.83	0.21	0.32	0.73
	RR:DF:SD	0.63	0.65	0.99	0.43	0.65	0.63	0.55	0.70	0.95	0.44	0.50	0.74	1.10	0.36
<i>Fraxinus pennsylvanica</i>	RR	8.35	0.00	12.61	0.00	0.23	0.80	0.07	0.93	0.06	0.94	0.00	1.00	0.60	0.58
	DF	0.19	0.83	0.67	0.55	0.01	0.99	0.27	0.77	0.24	0.79	0.11	0.90	0.97	0.43
	SD	1.34	0.34	0.40	0.57	0.05	0.84	0.98	0.40	0.04	0.85	0.07	0.81	0.35	0.60
	RR:DF	0.78	0.56	1.52	0.26	0.87	0.51	0.87	0.51	0.58	0.68	0.84	0.52	1.49	0.26
	RR:SD	0.25	0.79	1.31	0.34	0.38	0.70	3.03	0.12	1.37	0.39	0.93	0.44	1.00	0.42
	DF:SD	0.07	0.93	0.14	0.87	0.38	0.70	0.39	0.69	0.39	0.70	0.07	0.94	0.09	0.92
	RR:DF:SD	0.44	0.78	0.18	0.95	2.08	0.11	0.34	0.85	1.31	0.29	0.57	0.69	0.06	0.99

Statistically significant values ($P < 0.05$) are given in bold. * or ** indicate that model was square-root or log transformed, respectively.

2.4.4 Traumatic tree responses after reduction pruning in relation to stress treatments

In 2017, two years after reduction pruning of the main tree stem, epicormic branch occurrence and development close to the pruning cut were significantly and negatively affected in *Celtis* trees that faced root-reduction stress. However, this effect was not significant in *Fraxinus* trees (Table 2.2). In *Celtis*, epicormic branch number, average height, volume, and the height of the tallest epicormic branch started to decline when trees experienced a 75% root reduction (Figure 2.4). Although not statistically significant, root reduction also influenced the area of wood discoloration at the cutting point on *Celtis*. By contrast, root reduction, defoliation, and stem damage did not have an impact on the wood discoloration at the cutting point of *Fraxinus* (Table 2.2).

2.5 Discussion

2.5.1 Tree vigor and traumatic responses after reduction pruning

The results from our study showed that the epicormic branching responses of trees after a main-stem reduction differed between tree species and were related to tree vigor (Table 2.1; Figure 2.1 and 2.2). Trees with greater APG and ASG had a greater number and volume of epicormic branches, and taller epicormic branches. This finding indicates that tree vigor before pruning is a significant factor influencing the occurrence and development of epicormic branches at the cutting point after pruning. Nicolini et al. (2001) and Colin et al. (2008) previously reported this pattern following a tree-stand thinning; however, the trend was diametrically opposed to our study as moribund trees were more likely to produce epicormic branches than dominant trees. One reason for the difference between our study and previous studies could be related to differences in the functional role of epicormic branches between the studies (Bégin and Filion, 1999; Meier et al., 2012). Whereas the trees in Nicolini et al. (2001) and Colin et al. (2008) produced adaptive epicormic branches on the trunk that enhanced foliage area

in the absence of wounds, the trees in our study produced traumatic epicormic branches to rebuild the loss of crown leaf area after reduction of the main stem. Although both epicormic branch processes require adequate stored reserves for development (Harrington, 1989; Morisset et al., 2012), it appears that the moribund trees in our study did not have enough reserves to allow adequate crown rebuilding at the cutting point (Ramirez, 2017). Interestingly, two years before the main-stem reduction, stored reserves in the roots of both *Celtis* and *Fraxinus* were significantly higher in trees with lower growth rates (Ramirez, 2017), which could indicate that stored reserves were not only mobilized and used for epicormic branching, but also for compartmentalization of wounds after pruning. Several authors have reported that reduced tree vigor decreases wound occlusion (Nicolescu et al., 2013; Dănescu et al., 2015; Sheppard et al., 2016); therefore, we expected that the discolored area of the wood would increase with lower tree vigor. Surprisingly, two years after reduction of the main stem, the discolored area of the wood at the cutting point was significantly smaller in trees with lower ASG rates. In the event of a main-stem reduction and in relation to tree vigor, our results suggest that a trade-off between epicormic branching and wood discoloration may occur at the cutting point to restore the loss of biomass. Thus, trees with lower vigor may invest in limiting the expansion of the wound over rebuilding the crown. In contrast, trees with greater vigor may invest preferentially in the creation of new biomass at the expense of limiting wound expansion. However, differential responses were observed in crown architectural physiology of *Celtis* when trees fell below an ASG threshold value of 0.5 mm (Figure 2.2). Indeed, we observed that *Celtis* trees with reduced ASG underwent several crown die-back events, and in some cases showed signs of retrenchment with mortality of the retained lateral branch associated with expansion of the discolored wood area, coupled with the occurrence and development of epicormic branches on the lower part of the trunk. On the contrary, crown development in *Fraxinus* trees continued toward recovery and growth without indication of die-back, suggesting that *Fraxinus* trees with lower growth didn't reach the threshold of traumatic crown adaptation. These observations suggest that trees with lower growth and reach the

threshold of crown adaptation have developed several different ways to survive following reduction of the main stem (Drénou, 2000; Dujesiefken et al., 2005; Drénou et al., 2015). If stored reserves are sufficient to develop an efficient, defensive compartmentalization process around the pruning wound, trees will attempt to regenerate and re-establish the crown at the cutting point by epicormic branching in relation to the remaining available stored reserves (Smith, 2006). Otherwise, the discolored area of the wood at the cutting point, as well as crown die-back, will continue to expand and trees will attempt to rebuild a new crown on part of the trunk below the initial crown, before the entire system dies (Dujesiefken et al., 2005; Drénou et al., 2015).

By examining differences in the traumatic responses at the cutting point after reduction of the main stem of a tree, our study showed contrasting dynamics between species (Table 2.1, Figure 2.3). The higher the growth rate before pruning, the greater the number of epicormic branches produced in *Celtis* trees after pruning compared to *Fraxinus*, which suggests that the potential of the axillary bud bank of *Celtis* is higher than that of *Fraxinus* (Meier et al., 2012). However, although the epicormic branch height of *Celtis* was slightly greater compared to *Fraxinus*, the volume of the epicormic branches produced to rebuild the crown was lower and the area of wood discoloration was larger. Considering the trade-off discussed above, it appears that species with rapid and efficient compartmentalization can invest more resources in producing new growth compared to species with slow and less efficient compartmentalization. This observation was particularly noticeable in trees that had lower vigor before stem reduction, as the number, height, and volume of epicormic branches in the species with less efficient compartmentalization (*Celtis*) sharply decline compared to the species with more efficient compartmentalization (*Fraxinus*). Similar results have been found regarding species composition along a transect from an electrical power line corridor with repeated cuttings every five years, to the forest edge and forest interior with no growth disturbance (Luken et al., 1992). Whereas the frequency of *Celtis* was 80% and

70% in the forest interior and at the edge, respectively, the frequency declined to 40% in the maintained corridor. By contrast, *Fraxinus* had constant frequencies of 95%, 80% and 75%, at the forest edge, and in the forest interior and corridor, respectively (Luken et al., 1992). From an individual-survival perspective, the results suggest that although trees with less efficient compartmentalization can survive a reduction of the main stem, these trees have reduced stress-recovery resilience at the cutting point compared to trees with more efficient compartmentalization. These results are consistent with the recommendation of many authors to divide tree species into two main groups prior to pruning, according to compartmentalization efficiency (Drénou, 1999; Dujesiefken and Stobbe, 2002; Dujesiefken et al., 2005, 2016; Grabosky and Gilman, 2007; Gilman, 2011).

2.5.2 Tree vigor and traumatic responses in relation to stress treatments

Detailed dendrochronological analyses by Vitali et al. (2019) have previously demonstrated the influence of root-, defoliation-, and stem-damage treatments on the relative ASG of both *Celtis* and *Fraxinus* trees, two years after the last stress treatment. By using the APG and ASG, our study confirmed that tree vigor can shift in importance with respect to stress treatment and species (Table 2.2). In this study, the 75% root reduction treatment was the only one that significantly decreased the APG and ASG in both species two years after the last application. This finding highlights the dominant influence of root-reduction stress on tree vigor (Table 2.2; Figure 2.4). From a management perspective, it appears that a 37% removal of the root system is the threshold above which the health and vigor of trees may be impacted in the long term (Pretzsch et al., 2016). More specifically, for *Celtis*, root reduction was not the sole stress affecting tree vigor since its APG was also affected by defoliation (Table 2.2; Figure 2.4). This suggests that *Celtis* trees may have a greater sensitivity to stress and exhibit a longer period for wound isolation following stress episodes compared to

Fraxinus. This may be related to exhaustive and demanding compartmentalization and repair processes, as discussed above. This difference in species tolerance to damage is clearly observed when examining the tree-ring chronologies of both species (see Figure 3 in Vitali et al., 2019). Most *Celtis* trees showed a decline in growth immediately following the first application of stress treatment and this decline lasted for several years. By comparison, most *Fraxinus* showed a decline in growth only following the second stress treatment application and recovered the next year. However, as control trees for each species experienced, to a lesser extent, similar growth trends to those of treated trees, we suggest that control trees were also impacted by the stress treatments, and especially those inflicted on the root system. Indeed, taking into account the size of trees prior to the stress treatments, the plantation distance between the trees in our study, and the capacity of lateral roots to extend three times farther from the trunk than the branches (Hodgkins and Nichols, 1977; Watson and Himelick, 1982; Gilman et al., 1987), it appears that the root reduction applied to the treated trees surely impaired the root system of adjacent trees, and consequently, their growth. Since *Celtis* trees seem to be more sensitive to root reduction and take more time to recover from the stresses, this could explain why this species showed generally lower vigor than *Fraxinus* species prior to stem reduction.

Interestingly, although the species exhibited differences in vigor prior to reduction of the main stem, only *Celtis* trees that underwent a 75% root reduction demonstrated a significantly impaired ability to rebuild the crown at the cutting point (Table 2.2, Figure 2.4). This result indirectly confirmed that *Celtis* trees with signs of crown mortality were those with root systems subjected to the most damage. However, this result also provided evidence of resilience in both species and an ability to recover from loss of part of the main stem despite damage. Nonetheless, the tripling and quadrupling of epicormic branch height and volume, respectively, that we observed between *Celtis* and *Fraxinus*, indicates that such resilience is dependent on tree vigor status and the ability to compartmentalize before pruning.

2.6 Conclusion

Our study showed that the more vigorous and healthier the trees are, the more they will epicormic branch at the cutting point if a part of the main stem is reduced. For trees with lower vigor, the number, height, and volume of epicormic branches were influenced by the efficiency of the tree species to compartmentalize the pruning wound. However, past a threshold of weak vigor, epicormic branch initiation at the cutting point appears to be compromised, likely due to retrenchment of the crown. More generally, less efficient compartmentalizing species have a greater sensitivity to damage commonly occurring in urban areas and a greater area of discolored wood at the cutting point after pruning. In the context of the electrical distribution network, where trees are pruned regularly, the results of this study suggest favouring the plantation of more efficient compartmentalizing species (Gilman, 2011) to limit cavity formation and to ensure greater mechanical strength. Also, if management objectives are to optimize pruning cycles by developing a model of re-growth (Follett et al., 2016), an assessment of tree vigor before pruning should be conducted to identify trees with lower vigor and better predict the return pruning time. Visual methods (Mattheck and Breloer, 1994) or terrestrial lidar (Lecigne et al., 2018) could be used for this purpose, as long as the number of trees to monitor is reasonable. Airborne lidar (Jutras et al., 2009), combined with multi/hyperspectral imagery at high resolution (Degerickx et al., 2018) or other imagery techniques (e.g., fluorescence imagery, Hermans et al., 2003), could be used when monitoring a large number of trees.

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2.9 Supporting information



Figure 2.S1 Illustration of the dissected and analyzed trunk sections of *Fraxinus pennsylvanica* (left panel) and *Celtis occidentalis* (right panel). The Black line, parallel with and 15 cm from the pruning cut, represents the limit of the surface area studied. The surface delineated in red represents the wood discoloration area associated with the reduction pruning wound. Each area of discoloration was normalized by dividing it by the length of the cross-sectional pruning cut (yellow arrow).

CHAPITRE III

OPTIMIZING REDUCTION PRUNING OF TREES UNDER ELECTRICAL LINES: INFLUENCE OF THE INCLINATION OF THE RETAINED LATERAL BRANCH BEFORE PRUNING ON TREE CROWN RESTORATION PROCESS

Perrette, G.^{1,2,3}, Delagrangé, S.^{2,3}, Messier C.^{1,2,3}

- ¹ Department of Biological Sciences, Université du Québec à Montréal, Centre Ville Station, P.O. Box 8888, Montreal, Qc, H3C 3P8, Canada
- ² Institute of Temperate Forest Sciences, Université du Québec en Outaouais, 58 Rue Principale, Ripon, Qc J0V 1V0, Canada
- ³ Center for Forest Research, Université du Québec à Montréal, Centre-ville Station, P.O. Box 8888, Montréal, Qc, H3C 3P8, Canada

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3.1 Abstract

Reduction pruning of the main stem is commonly performed during the maintenance of the electricity distribution network to train trees to coexist with wires. Understanding tree development and the crown restoration process are important for maintaining healthy and safe trees as well as optimizing the pruning return interval. In this study, the influence of reduction pruning intensity (low and high) and seasons (summer, late summer and winter) on annual primary and secondary growth (APG and ASG, respectively) were investigated on 56 eleven-year-old Pennsylvania ash trees (*Fraxinus pennsylvanica* ‘Marsh’) within a controlled nursery environment. We also examined the influence of the inclination of the retained lateral branch (RLB) of the reduction pruning cut, measured prior to pruning, on RLB growth, epicormic branch development, and wound compartmentalization after pruning. During the second growing season after reduction pruning, the APG and ASG of tree decreased with pruning intensity, but seasonal influences were minor. A more upright inclination of the RLB prior pruning increased both RLB growth and the wound-closure rate after pruning. Although a reduced number of epicormic branches was associated with a more upright inclination of RLB, the result was not statistically significant. Adoption of a reduction pruning of low intensity of the main stem, while avoiding plagiotropic RLBs, is recommended to maintain tree health and limit post-traumatic tree responses.

Keywords: CODIT, Electricity Distribution Networks, Maintenance Return Interval, Pruning Intensity and Season, Epicormic Branch Growth, Tree Development, Utility Arboriculture, Vegetation Management.

3.2 Introduction

Reduction pruning of the main stem is commonly used by certified practitioners during the tree-training maintenance of power lines, when trees are directly under the wires. This process encourages the occurrence and establishment of scaffold limbs near the cutting point to obtain a "V" bilateral crown form at maturity (Millet and Bouchard, 2003; Gilman, 2011; Lecigne et al., 2018). The first scaffold limb is generally located between 2 and 4 m from the ground to circumvent wires located 7 to 9 m above the ground (Millet and Bouchard, 2003). Our current understanding of best practices for reduction pruning suggests that the diameter of the retained lateral branch (RLB) should comprise at least one-third of that removed to stimulate recovery of apical dominance of the RLB (Gilman and Lilly, 2002 cited in Grabosky and Gilman, 2007) and the diameter of the pruning cut should not exceed 5 cm for species with less compartmentalization ability or 10 cm for species with efficient compartmentalization ability to limit risk of decay at cutting point (Dujesiefken and Stobbe, 2002; Dujesiefken et al., 2005, 2016; Gilman, 2011). However, the space released within the crown structure of the tree undergoes epicormic branch recolonization within a few years after a reduction pruning intervention (Goodfellow et al., 1987; Follett et al., 2016) in order to rebuild the leaf area loss of the crown (Deal et al., 2003) and restore the energy balance between both the above- and below-ground systems (Valentine, 1985). As a result, trees require repeated pruning for epicormic branch removal to maintain clearance standards (Goodfellow et al., 1987; Millet and Bouchard, 2003; Follett et al., 2016; Lecigne et al., 2018). Such repeated maintenance entails major expenses (Goodfellow et al., 1987; Millet, 2012) that are influenced by the rate of epicormic branch growth, number of epicormic branches to be removed, and volume of the epicormic branches to be chipped (Nowak, 1990; Browning and Wiant, 1997). Consequently, a better understanding of epicormic branch and tree development after reduction pruning of the main stem is needed to optimize maintenance of the

distribution network and minimize the impact of pruning on the tree, while maintaining healthy trees that are safe for residents and local infrastructure.

In classic silvicultural practices, the health of trees, in terms of annual primary growth (APG) and annual secondary growth (ASG), has been shown to be affected by both pruning intensity (Uotila and Mustonen, 1994; Neilsen and Pinkard, 2003; Alcorn et al., 2008; Maurin and DesRochers, 2013; Hevia et al., 2016) and pruning season (Maurin and DesRochers, 2013) involving the removal of the lower primary branches to improve bole value. However, it is largely unknown whether similar factors could impact tree health when the main stem is reduced (Langstrom et al., 1990) as is often the case in urban tree management.

Pruning creates wounds and dysfunctional wood at the cutting point, and may provide entry for microorganisms of decay that induce cavity formation over time and alter the health, mechanical strength, and safety of the tree (Dujesiefken and Stobbe, 2002; Dujesiefken et al., 2016). The wound compartmentalization process has been well described since the CODIT (Compartmentalization of decay in trees) model was established by Shigo and Marx (1977). At the cutting point, the area of the exposed wound is closed and the spread of wood discoloration in the internal structure is contained through the formation of reaction zones (Gilman, 2011; Dujesiefken et al., 2016). Both directional pruning and the intensity of pruning have been shown to influence compartmentalization of the pruning wound (Dujesiefken and Stobbe, 2002; Dahle et al., 2006; Grabosky and Gilman, 2007; Dujesiefken et al., 2016; Perrette et al., Chapter 1) as well as epicormic branch development (Goodfellow et al., 1987; Millet and Bouchard, 2003; O'Hara et al., 2008; DesRochers et al., 2015; Follett et al., 2016; Perrette et al., Chapter 1). However, few studies have examined the overall integrated restoration process of the tree crown after pruning (Perrette et al., Chapters 1 and 2) in relation to the inclination of the RLB prior pruning (Wareing and Nasr, 1961).

Branch inclination has been shown to affect ASG in fruit trees (Wareing and Nasr, 1961). However, little information is available regarding the influence of the inclination of the RLB prior reduction pruning of the main tree stem on subsequent epicormic branch production and wound compartmentalization (Grabosky and Gilman, 2007).

The goal of this study was to examine the effect of different pruning intensities and pruning seasons on ASG of trees and the APG of the RLB, and assess the influence of the inclination of the RLB prior pruning on the APG of the RLB, epicormic branch development, and wound compartmentalization following reduction pruning. This study was carried out in a controlled nursery environment to minimize any confounding influences associated with urban environmental conditions that could affect tree growth responses (Jutras et al., 2010).

3.3 Material and methods

3.3.1 Study site

The study was conducted 40 km northeast of Montréal, at the Montréal Municipal Nursery in Assomption, Québec, Canada (45°48'N 73°25'W). In this area, the climate is continental and humid, with hot summers and cold winters. Between 1970 and 2000, the average annual temperature was 5.3°C and the average annual precipitation was 1018.7 mm with a mean annual snow cover of 208.9 cm (Environment Canada 2018, Assomption weather station). The mean daily maximum and minimum temperatures are 10.5°C and 0°C, respectively; the maximum and minimum yearly temperatures on record are 37.2°C and -43.3°C, respectively. Annually, there is an average of 1,958 hours of sunshine, 2,804 degree-days below 10°C, and 1,099 degree-days above 10°C. Temperatures below 0°C occur between October and April and the snow season commonly extends from mid-November to the end of March (Boyer et al., 1985). The texture of the soil consists of clay and clay mixed with fine sand subsoil.

3.3.2 Experimental design and pruning treatments

The experiment took place in 2015 in an existing plantation alignment composed of 56 Patmore and Prairie Spire green ash trees (*Fraxinus pennsylvanica* Marsh). The trees were 11 years old, 5.6 to 7.3 m (mean = 6.4 ± 0.3 m SD) tall, and had a diameters at breast height (dbh) of 5.7 to 9.7 cm (mean = 7.9 ± 1.0 cm SD).

Further details on the implementation of the field design and pruning treatments can be found in Perrette et al. (Chapter 1). The overall experiment consisted of 6 reduction pruning and 1 control treatments arranged in a random-block design, with eight blocks, and seven trees per block. Two treatments that differed in the reduction intensity of the main stem were applied 2 to 2.5 m and 3 to 3.5 m above ground (hereafter referred to as high and low intensity reduction pruning, respectively) to simulate a prescribed corridor zone of 2.5 m around a fictitious power distribution network located 7 m above the ground (Figure 3.1) during three distinctive seasons: early July, early September, and early December (hereafter referred to as summer, late summer, and winter, respectively). Because the retained lateral branch diameter relative to the parent axis diameter affects the surface area of decay after reduction pruning (Eisner et al., 2002a; Gilman and Grabosky, 2006), we tried to keep the aspect ratio of the main stem reduction pruning within a small range across trees in all reduction pruning and control treatments (from 0.38-0.46). To obtain this range, we first selected similar branch unions on each tree for both pruning intensities and prior to assigning random block treatment. For each branch union, the parent axis and RLB diameters were measured 10 mm above the branch bark ridge to determine the aspect ratio. RLBs with either included bark or codominant aspect were not selected. Trees were assigned as controls if both pruning intensities were applicable regarding the aspect ratio (Figure 3.1), whereas season treatments were randomly assigned to trees on which only one aspect ratio of pruning intensity was applicable. For each reduction pruning treatment of the main stem, only one cut was made using a hand saw, in compliance with recommendations of the American National Standards Institute (ANSI, 2008). The

diameter of the pruning wound ranged from 5 to 7.5 cm (mean = 6.1 ± 0.8 cm SD) and 4.2 to 6.6 cm (mean = 5.2 ± 0.7 cm SD) for the high- and low-intensity pruning treatments, respectively. The amount of removed biomass was visually estimated by two assessors, and ranged from 60% to 72% (mean = 67 ± 4 % SD) for the high-intensity pruning treatment and 35% to 52% (mean = 45 ± 4 % SD) for the low-intensity pruning treatment.

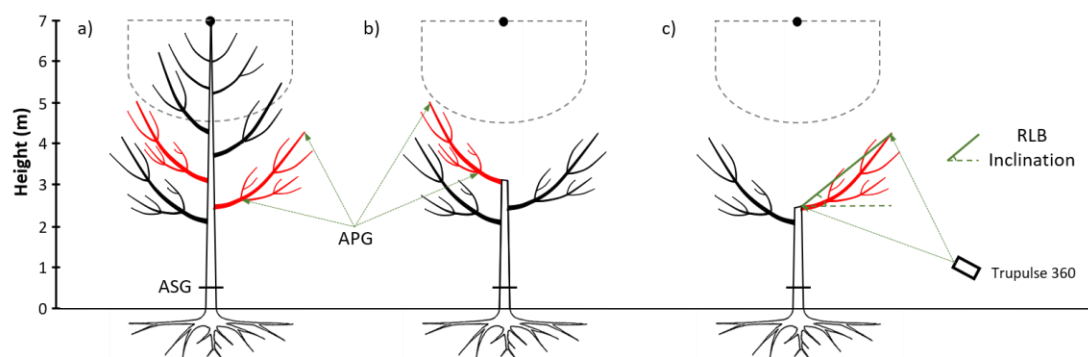


Figure 3.1 Illustration of tree control (a) and reduction pruning treatments of the main tree stem at 3-3.5 (b) and 2-2.5 m (c) above the ground. Black filled circle represents a wire running 7 m above the ground and dashed grey line the security corridor. Each control tree had two branches (hereafter referred to as RLB) with similar aspect ratio to that of RLB in both reduction pruning treatments. Trees ASG of both control and pruning treatments were obtained from dendrochronology analyses on circular cross-sections collected 0.4 m above ground (a) and APG of RLB from measuring the last two years of growth following intervention (a and b). The RLB inclination prior to intervention was determined by using a trupulse 360 (c).

3.3.3 Data collection

3.3.3.1 Tree ring data and analyses

Trees were harvested in 2017 and circular cross-sections were collected for each tree at a height of 0.4 m (Figure 3.1). Cross-sections were progressively polished with sandpaper (up to 400 grit) and scanned at 2400 dpi. Annual ring widths were measured

on three radii per cross-section using CooRecorder 7.6 software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). CDendro software (Cybis Elektronik & Data AB) was then used to cross-date individual series and average them for each tree. Ring-width data were used to calculate the diameter of each tree prior to pruning. Cumulated ring-width data from 2015 to 2017, corresponding to the growth period between the pruning intervention and sample collection, were subsequently used to determine ASG.

3.3.3.2 Attributes of the RLB

In mid-August 2015, inclination of the RLB of main stem reduction pruning and that of both RLBs on the control trees were measured using a handheld laser rangefinder/clinometer (Follett et al., 2016; Trupulse® 360, Laser Technology Inc., Centennial, Colorado, USA). Laser measures were collected from the upper part of the branch insertion to the terminal bud of the primary branch order (Figure 3.1). The terminal bud was then flagged to spot the 2015 bud scar position in the future.

At the time of harvest in 2017, APG of the RLB, corresponding to the period between 2015 and 2017, was measured with a 30-cm ruler. Measurements were taken from the upper part of the 2015 flagged bud scar to the upper part of the 2017 terminal bud of the primary branch order (Figure 3.1).

3.3.3.3 Epicormic branch inventory

All deferred or proleptic live epicormic branches and immediate or sylleptic live epicormic branches (Bégin and Filion, 1999) were counted and measured during late summer 2017, when initiation or growth exceeded the height of the reduction pruning cut. Growth-unit length and the median diameter of each epicormic branch were recorded with a ruler and calipers. The total height and volume per epicormic branch were

obtained by adding the growth units of primary order length and growth-unit volume of all branch orders. The mean number and volume of epicormic branches, and the tallest epicormic branch per treatment were determined by averaging the number, volume, and length data for each tree, respectively. The epicormic branch mean height was obtained by averaging epicormic branches height per tree prior averaging per treatment.

3.3.3.4 Closure rate of the pruning wound

In 2015, immediately after reduction pruning, we measured the vertical length (parallel to the retained lateral branch of the main stem reduction pruning) and horizontal width of the pruning wound to the nearest mm to calculate the surface area of the wound as an ellipse. Both measurements were made crossing the wound pith. In 2017, two growing seasons after the reduction pruning intervention, we retook the measurements to calculate the surface area of the wound not fully closed by the callus tissue. The wound-closure rate was expressed as a percentage of the area of the surface wound immediately after pruning.

3.3.3.5 Discolored wood area following reduction pruning

In 2017, at the end of the growing season, the section of the trunk bearing the wound from the pruning treatments was dissected with a sliding table saw along a radial longitudinal plane of 30 cm, bisecting both centers of the pruning wound and the RLB. Dissected sections were progressively polished with up to 400-grit sandpaper and scanned at 2400 dpi. The area of discolored wood for each pruning wound was delineated, and its surface area was calculated based on pixel counts using Adobe Photoshop CC 2018 (Adobe Systems, Inc., San Jose, California, United States). All areas of discolored wood were normalized by dividing them by the length of the cross-sectional area of the pruning cut. The final area of discolored wood per pruning wound was computed as the average of the two halves.

3.3.4 Statistical analysis

Linear mixed effects models were used to predict tree ASG and RLB APG as a function of pruning intensity and pruning season. Sampling block was included in the models as a random effect. First, we tested for differences between cultivars, and because results were similar (Figure 3.S1), the cultivars were pooled in final models. As no interaction between pruning intensity and season was found in any model, those results are not presented. Wilks and Brown–Forsythe tests were used to test assumptions of normality and homoscedasticity, respectively.

An analysis of covariance (ANCOVA) was used with RLB inclination prior pruning specified as a covariate to examine the effect of the inclination of the RLB over time on the APG, and epicormic branch (height, number, volume, tallest) and wound (closure rate and area of discolored wood) responses. Because the APG of RLB was found to be similar among pruning seasons (see Section 3.1) and due to the large range of RLB inclinations, only the intensity treatments were included in the analyses. Wilks and Brown–Forsythe tests were used to test assumptions of normality and homoscedasticity, respectively. The data were transformed using a Box–Cox model (Box and Cox, 1964) when the residuals did not meet these assumptions; the results and predicted values were subsequently back-transformed for graphical presentation. Because zero values occurred in the transformed data model, a value of 1 was added to each count. In preliminary models, the interaction between pruning intensity and RLB inclination was tested. Because the interaction was not significant, the interaction term was not included in the final model. One tree in each pruning intensity treatment was removed from the analysis as it was considered to be an outlier due to inconsistency in the data with respect to many of the variables. All statistical analyses were conducted using JMP software, version 14.0.0 (SAS Institute, Cary, NC, USA).

3.4 Results

3.4.1 Tree growth after reduction pruning of the main stem

In 2017, two years after reduction pruning, the cumulated ASG for all pruning treatments was lower than that of control trees (Figure 3.2; results not shown). In all seasons, a higher intensity of reduction pruning significantly decreased the cumulated ASG ($F_{1,7} = 15.82$, $p = 0.0053$). However, pruning season had no effect on cumulated ASG ($F_{2,14} = 0.33$, $p = 0.7199$).

Similarly, the cumulated APG of the RLB was significantly decreased with a greater reduction pruning intensity. ($F_{1,7} = 13.68$, $p = 0.0077$). However, although pruning season did not affect the cumulated APG of the RLB, APG values of pruned trees were 2-fold greater than those of control trees ($F_{3,21} = 15.22$, $p < 0.0001$).

3.4.2 Post-traumatic responses to reduction pruning in relation to pruning intensity and the inclination of the RLB

In 2017, two years after reduction of the main stem, a significant influence of reduction pruning intensity was detected on the cumulated APG of the RLB, and the number, height, and volume of epicormic branches, as well as the tallest epicormic branch and the area of wound discoloration. However, reduction pruning intensity did not affect the wound closure rate (Table 3.1).

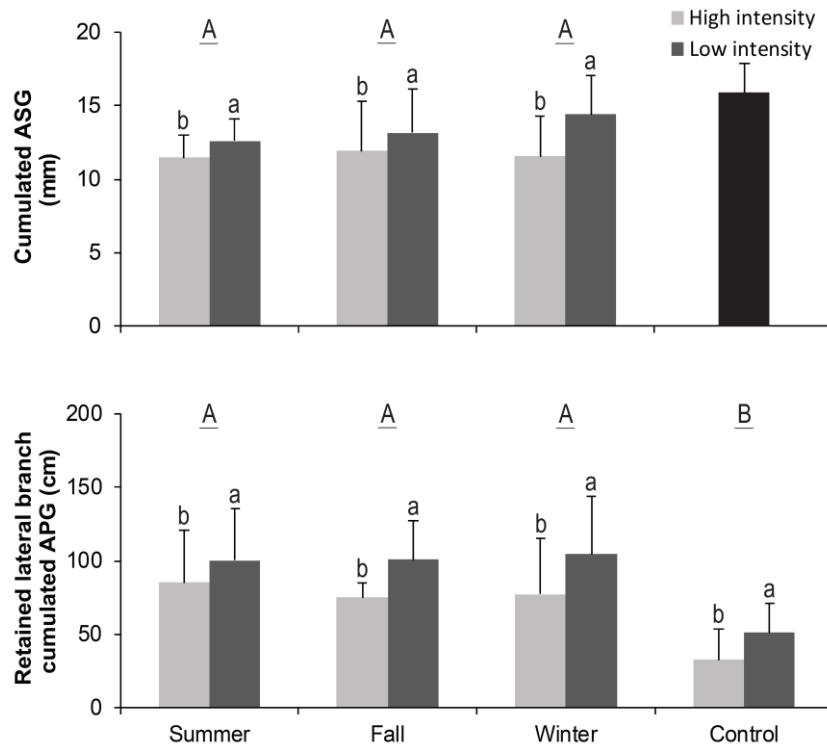


Figure 3.2 Cumulated (\pm SD) ASG of the main stem and APG of the retained lateral branches after reduction of the main stem from 2015 to 2017 for pruning intensity and season. For differences between intensities within seasons, different letters above the bars indicate significant differences based on paired t-tests. For differences between seasons within intensities, capital letters above the bar pairs indicate significant differences based on Tukey's HSD post-hoc tests ($p > 0.05$). Despite having been excluded from analyses of ASG, controls are shown in the graph in dark black. However, both preserved RLBs in control trees were included in APG analyses.

Table 3.1 Summary results of ANCOVA models comparing the retained lateral branch, epicormic branch and wound compartmentalization responses in 2017 after reduction of the main stem between intensity (low and high). The inclination of the retained lateral branch (INC) before reduction pruning intervention in 2015 was specified as a covariate.

	Model	Intensity	INC	R^2
Retained lateral branch				
Cumulated APG	0.0055	0.0170	0.0104	0.27
Epicormic branch				
Number	<0.0001	<0.0001	0.0879	0.58
Height	0.0337	0.0211	0.1077	0.15
Volume*	<0.0001	<0.0001	0.7307	0.47
Tallest	0.0005	<0.0001	0.2791	0.30
Wound compartmentalization				
Closure rate*	0.0157	0.5310	0.0073	0.18
Discolored wood area*	0.0002	<0.0001	0.8458	0.33

* Indicates that data were transformed using Box–Cox transformations prior to analyses. Significant effects ($p < 0.05$) are indicated in bold.

The inclination of the RLB prior reduction pruning had a significant positive effect on the cumulated APG of the RLB and the closure rate of the wound after pruning (Table 3.1, Figure 3.3). Although not significant, a higher inclination of the RLB was also associated with a decreased number of epicormic branches following pruning (Table 3.1, Figure 3.3). However, the inclination of the RLB didn't influence the height or volume of epicormic branches, or the area of wound discoloration (Table 3.1).

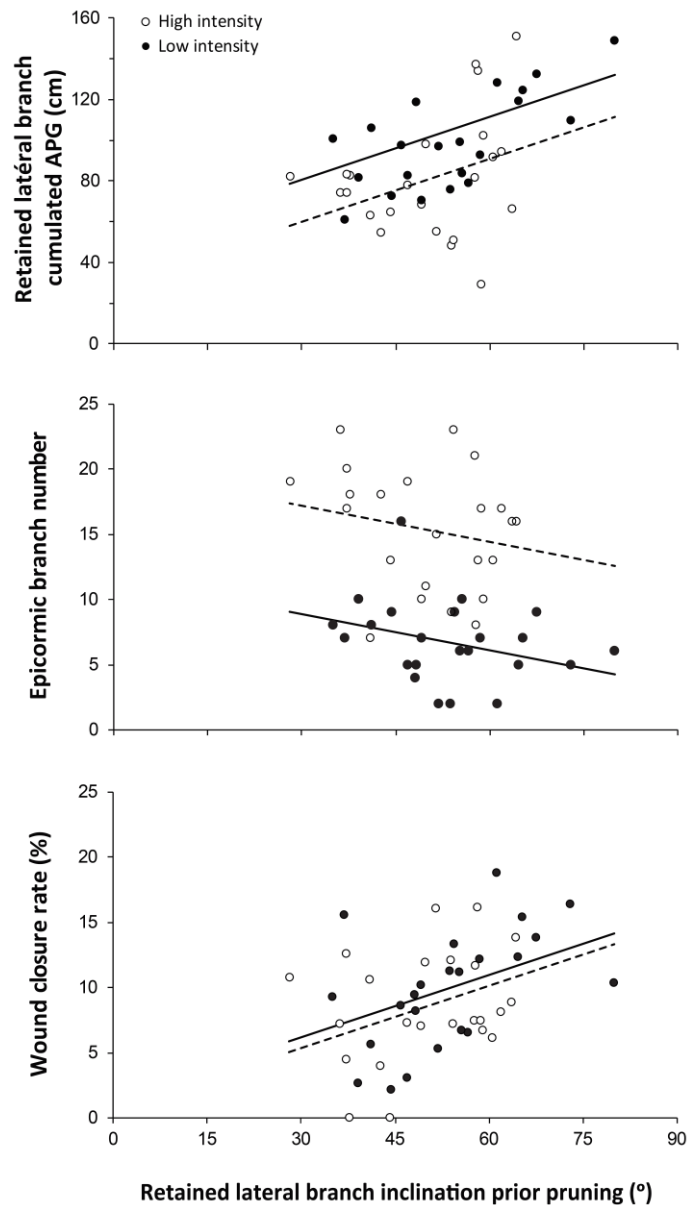


Figure 3.3 Cumulated APG of the retained lateral branch from 2015 to 2017, as well as the number of epicormic branches and wound-closure rate in 2017 in relation to the inclination of the retained lateral branch, as measured in 2015 before reduction of the main stem. Because the APG of RLB were found to be similar between pruning seasons and to cover a large range of RLB inclinations, only the intensity treatments were included in the analyses. Dashed black lines indicate means of the high intensity relationships and solid black lines are means of the low intensity relationships. Data for the wound-closure rate were transformed before ANCOVA using Box-Cox transformations with the following parameter values: $\lambda = 0.2510$, $\alpha = 6.4843E-2$.

3.5 Discussion

3.5.1 Main-stem reduction pruning treatments and tree growth

The results of our study showed that, after reduction pruning, the effect of pruning season on tree growth was of lesser importance than the intensity of pruning (Figure 3.2). Compared to reduction pruning during the dormant season, pruning during the growing season to raise the crown of the main stem has been reported to have only a minor effect on the primary and secondary growth of trees two years after the intervention (Maurin and DesRochers, 2013). In our study, the APG and ASG were found to be similar between pruning seasons, for both intensities of reduction pruning, after the second post-intervention growing season. Although, this difference in results between our study and those of Maurin and DesRochers (2013) could be due to the type of pruning, Fini et al. (2015) found no differences in tree growth following a reduction or removal pruning treatment. Therefore, this difference in growth results between our study and that of Maurin and DesRochers (2013) appears to be due to a tree-recovery delay related to the different pruning interventions (O'Hara et al., 2008). In our study, summer pruning took place before winter pruning, which allowed for 2.5 growing seasons for the trees to restore the energy balance between the above- and below-ground systems. By contrast, trees only had 1.5 growing seasons in the study by Maurin and DesRochers (2013) because summer pruning occurred after winter pruning. The combined results of crown-raising and reduction pruning of the main stem highlight the small, temporary effect of pruning season on tree development. These findings also demonstrate the importance of taking into account the variation in the time since pruning when determining any significant or non-significant seasonal effects on a long-term basis (O'Hara et al., 2008). Furthermore, these findings indicate that the trend of the effects of pruning season on tree development after pruning is similar among interventions completed on different parts of the tree.

Differences in tree development associated with intensity of pruning were more evident. In the context of silvicultural practices, a greater pruning intensity of lower primary branch orders has been shown to reduce the ASG of deciduous and coniferous trees (Uotila and Mustonen, 1994; Neilsen and Pinkard, 2003; Alcorn et al., 2008; Maurin and DesRochers, 2013; Hevia et al., 2016), likely by reducing the photosynthetic capacity of the tree and, consequently, the amount of root carbohydrate storage available for growth in the following growing seasons (Maurin and DesRochers, 2013). In our study, a similar process may have affected the ASG of trees after reduction pruning of the main stem (Figure 3.2). Nonetheless, in the context of silvicultural practices, although a higher pruning intensity was found to impact tree height more negatively compared to a lower pruning intensity, pruning has been shown to affect height growth less than diameter growth (Neilsen and Pinkard, 2003; Alcorn et al., 2008; Maurin and DesRochers, 2013) perhaps to maintain dominance while rebuilding carbohydrate storage, by recovering photosynthetic capacity (Amateis and Burkhardt, 2011). In our study, tree dominance exerted by the main stem apex was released and transferred to the RLB apex after reduction pruning to ensure continuity during crown ontogeny (Wilson, 2000). This could explain why the APG of RLB was 2-fold higher on trees that underwent either intensity of reduction pruning compared to lateral branches of similar size on the control trees (Figure 3.2). However, although the reduction pruning significantly and positively influenced the subsequent APG of the RLB, the data did not offer a clear indication as to whether this effect was exacerbated by pruning intensity. Indeed, in control trees, the APG of the RLB located between 3 and 3.5 m above ground was significantly greater than that observed for RLB located between 2 and 2.5 m above ground, and this difference was similar to that of pruned trees. Thus, the difference in RLB growth between the high and low intensity pruning treatments could be due to a difference in the height of the RLB in the crown (Remphrey and Davidson, 1994; Nikinmaa et al., 2003). Nonetheless, considering the negative effect of a higher pruning intensity on tree ASG compared to a lower intensity, and considering that both pruning intensities increased the APG of the RLB compared to control trees, a lower-intensity reduction pruning of the

main stem is recommended to limit more drastic impacts on overall tree growth development (Perrette et al., Chapter 1).

3.5.2 Tree crown restoration process in relation to reduction pruning intensity and the inclination of the RLB

By examining the traumatic responses of the tree after reduction pruning of the main stem, our study highlights the important roles of pruning intensity and inclination of the RLB prior pruning on the tree crown restoration process (Table 3.1). More detailed analyses by Perrette et al. (Chapter 1) have demonstrated the influence of pruning intensity on epicormic branch development, as well as compartmentalization of the pruning wound two years after a reduction pruning intervention. By using the inclination of the RLB as a covariate, our study confirmed that the traumatic responses of trees can change with respect to pruning intensity (Table 3.1). Compared to a lower reduction pruning intensity, a higher pruning intensity created a greater number, length, and biomass of epicormic branches, as well as a greater proportion of discolored wood at the cutting point and a possible reduced wound-closure rate, which could further reduce dominance recovery by the RLB, as discussed above (Table 3.1, Figure 3.3). In other words, a greater reduction pruning intensity induces a greater disorganization in the structure of the crown (Millet and Bouchard, 2003) in an attempt to restore the energy balance between the above- and below-ground systems (Valentine, 1985; Deal et al., 2003). Moreover, reduced compartmentalization of the pruning wound will be less effective in limiting the expansion of decay at the cutting point (Dujesiefken and Stobbe, 2002; Ow et al., 2013; Dănescu et al., 2015).

The crown restoration process at the cutting point was also shown to be significantly driven or influenced by the inclination of the RLB prior the main-stem reduction-pruning intervention, although to a lesser extent than pruning intensity (Table 3.1). At both pruning

intensities, a more upright inclination of the RLB at pruning time was associated with a greater recovery of the APG of the RLB two years after intervention (Figure 3.3). Wareing and Nasr (1961) and Wilson (2000) have previously reported this gravimorphism effect, which is likely related to greater water flow conductivity on those branches with a greater vertical angle of orientation (Eisner et al., 2002b). However, this effect was impaired by reduction pruning intensity, as greater variability in RLB growth responses emerged with a higher pruning reduction intensity (Figure 3.3). Greater variability could be related to the fact that some trees in the higher pruning intensity treatment didn't have enough time to absorb the loss of biomass, highlighting again the harmful effects of a greater pruning intensity on short-term tree recovery. On the other hand, greater variability in response with a higher pruning intensity was also observed with regard to the number of initiated epicormic branches at the cutting point (Figure 3.3). This could explain why the result was not statistically significant despite the fact that the number of epicormic branches decreased with higher inclination of the RLB (Table 3.1, Figure 3.3). Using a low pruning intensity to reduce the main tree stem, coupled with a higher RLB inclination, may result in a lower but more predictable epicormic branch response. Considering that lower water flow conductivity occurs in RLBs at lower vertical inclinations (Eisner et al., 2002b), more water was likely retained at the cutting point after reduction pruning, which may have increased the epicormic branch number during the tree-crown restoration process (Harrington, 1989; Morisset et al., 2012). Interestingly, a lower inclination of the RLB before the main-stem reduction was associated with a significant decrease in the recovery of the exposed wound (Table 3.1, Figure 3.3). The inverse relationship between epicormic branch number and wound-closure rate reported in our study may suggest that although more water may have been retained at the cutting point in trees with a lower inclination of the RLB, this water may have been used for the development of epicormic branches to restore the crown, rather than closure of the pruning wound and the development of an efficient, defensive process against invading microorganisms. This could explain why the number of epicormic branches is higher following a heading or topping cut (i.e. when no RLB has been preserved) compared to a reduction cut (Goodfellow et al., 1987; Fini et al.,

2015; Follett et al., 2016), and results in a slower closure rate of the pruning wound (Fini et al., 2015). However, more analyses should be undertaken to further define these response effects.

Considering the similarities between individual trees and epicormic branch development (Raimbault and Tanguy, 1993; Dujesiefken et al., 2016), similar patterns related to pruning intensity and RLB inclination may affect re-epicormic branching following epicormic branch reduction during tree maintenance. Thus, re-epicormic branching could be reduced by using the same reduction pruning knowledge used for the main stem (i.e. low reduction pruning intensity on orthotropic RLB with a diameter at least one-third of that removed). Such an approach could help to lengthen the maintenance return interval when trees have reached maturity and need repeated pruning to maintain clearance standards (Goodfellow et al., 1987; Millet and Bouchard, 2003; Follett et al., 2016; Lecigne et al., 2018). However, further studies are needed to validate this approach to tree maintenance.

To improve knowledge aimed at optimizing the maintenance return interval when using main-stem reduction pruning, a similar study could be undertaken to maintain two RLBs at the cutting point. Indeed, considering our results and the fact that only one RLB was maintained, a second RLB, preferentially initiated opposite to the first one and perpendicular to the wire, could further limit water accumulation at the cutting point and epicormic branch development.

3.6 Conclusion

Our study showed that reduction pruning intensity of the main stem had a stronger effect on tree growth compared to the season when pruning was carried out. Using a low reduction pruning intensity should be considered to train trees to coexist with the electrical network, and preferentially in summer to limit the occurrence of epicormic

branches and decay at cutting point (Perrette et al., Chapter 1). Current knowledge on reduction pruning suggests that the diameter of the RLB should comprise at least one-third of that removed to stimulate recovery of the apical dominance on the RLB (Gilman and Lilly, 2002; cited in Grabosky and Gilman, 2007). In addition, our results suggest that reduction pruning of the main stem should be avoided on plagiotropic RLB. These considerations will also likely improve recovery of the pruning wound and limit epicormic branch initiation.

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3.8 References

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3.9 Supporting information

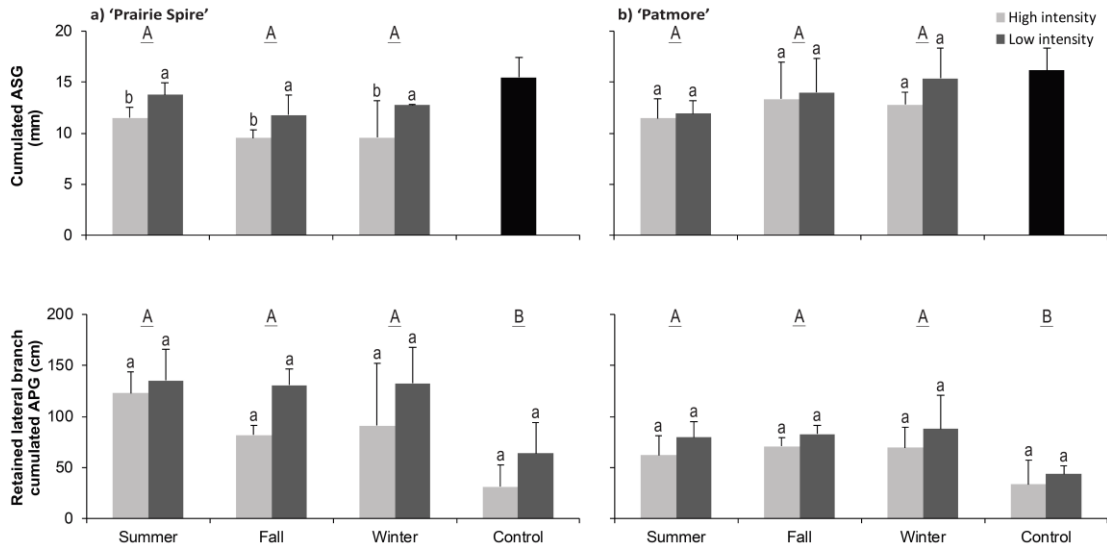


Figure 3.S1 Cumulated (\pm SD) tree ASG and APG of the retained lateral branch after reduction of the main stem from 2015 to 2017 for pruning intensity and season. (a) *Fraxinus pennsylvanica* 'Marsh'. 'Prairie Spire' (left panel) and (b) *Fraxinus pennsylvanica* 'Marsh'. 'Patmore' (right panel). For differences between intensities within seasons, different letters above the bars indicate significant differences based on paired t-tests. For differences between seasons within intensities, capital letters above the bar pairs indicate significant differences based on Tukey's HSD post-hoc tests ($p > 0.05$). Despite having been excluded from analyses of ASG, controls are shown in the graph.

CHAPITRE IV

CONCLUSION

4.1 Une vue d'ensemble de la thèse

La présence des réseaux électriques en milieu urbain est une contrainte majeure pour le développement génétiquement programmé de l'arbre (Millet et Bouchard, 2003). Pour permettre une cohabitation saine et sécuritaire avec les réseaux électriques, l'arbre est sujet à de multiples interventions de tailles tout au long de son cycle de vie. Cependant, ces interventions sont reconnues pour impacter drastiquement son développement par la mise en place de réitérations (Millet et Bouchard, 2003), tout en altérant sa stabilité mécanique par la formation de carie (Dahle et al., 2006). De par ses dispositifs expérimentaux uniques et le fait d'avoir des arbres assez vieux en milieu contrôlé pour faire ces expériences, cette thèse a permis de tester des connaissances propres à la gestion d'arbres évoluant dans un milieu sans contrainte pour les transposer à la gestion d'arbres avec contraintes afin d'améliorer notre compréhension du fonctionnement de l'arbre soumis à des stress de pertes d'une partie de sa couronne. Cette thèse marquera une avancée majeure dans notre compréhension de l'effet de l'élagage sur la réponse traumatique des arbres ayant un fort gradient de vigueur.

Dans le Chapitre 1, par rapport à un dispositif sans précédent qui visait à examiner simultanément la réponse réitérative et la compartimentalisation des blessures de taille à la suite d'une réduction de la tige principale de l'arbre et ce en fonction de l'intensité et du moment de l'année de la taille, nos résultats ont supporté l'hypothèse que l'intensité de suppression de la biomasse est le principal facteur influençant les réponses traumatiques. De plus, bien que dans une moindre mesure que l'intensité de

suppression, nous avons montré que les réponses traumatiques dépendaient de la saison à laquelle l'intervention avait été réalisée et que les résultats obtenus concordent avec les fluctuations saisonnières connues des réserves, mais également avec d'autres pratiques sylvicoles comme la coupe totale (Kays et Canham, 1991; Perrette et al., 2014) ou le rehaussement de la couronne de l'arbre (O'Hara et al., 2008; DesRochers et al., 2015). Ainsi, ce chapitre a permis de mettre en relief que quelque soit la nature de l'intervention de taille sur différentes parties de l'arbre, que la dynamique des réponses traumatiques en fonction de la saison d'intervention est indépendante de l'intensité pour reconstruire la perte de biomasse.

Dans le Chapitre 2, par rapport à un autre dispositif expérimental sans précédent qui visait à évaluer les effets d'un grand nombre de traitements et à fournir un aperçu unique des réactions communes des espèces d'arbres urbains aux contraintes mécaniques, nous avons montré que les réponses traumatiques à la suite d'une réduction de la tige principale de l'arbre dépendaient également de la vigueur des arbres avant l'intervention. Plus les arbres étaient vigoureux et en bonne santé avant l'intervention, plus ils ont réitéré vigoureusement au point de coupe comparativement à des arbres moins vigoureux. Cependant, la surface de bois décolorée au point de coupe des arbres les plus vigoureux était plus importante que celle mesurée chez les arbres les moins vigoureux. Nos résultats suggèrent qu'un compromis peut se produire entre le processus réitératif et celui de la compartimentation de la blessure lorsqu'une partie supprimée nécessite d'être restaurée. Ainsi, les arbres de moindre vigueur semblent préférentiellement investir leurs ressources pour limiter l'expansion de la surface de bois décolorée au point de coupe, mais au détriment de la mise en place du processus réitératif. Alors que l'effet inverse semble se produire chez les arbres les plus vigoureux. Une telle approche pourrait permettre aux arbres les moins vigoureux, d'investir le maximum de leurs ressources dans la lutte contre la propagation des microorganismes et ainsi éviter le dépérissement brutal dans la mesure où les microorganismes viendraient à se propager rapidement et que le niveau des réserves ne

permettrait plus de lutter efficacement. Néanmoins, pour les arbres les moins vigoureux, nos résultats indiquent que l'initiation et le développement des réitérations sont influencés par l'efficacité de l'espèce de l'arbre à compartimenter la blessure de coupe. L'espèce dont le processus de compartimentation fut le plus efficace a été plus résiliente à émettre un processus réitératif au point de coupe que l'espèce dont le processus de compartimentation présentait une efficacité moindre.

Finalement, dans le Chapitre 3, nous avons montré que la croissance de l'arbre et la reprise de la dominance apicale par l'appel-sève à la suite d'une réduction de la tige principale de l'arbre étaient principalement affectées par l'intensité de la réduction et que la saison d'intervention n'avait que peu d'effet. En outre, bien que dans une moindre mesure que l'intensité de la réduction, nos résultats ont montré que la reprise de l'appel-sève ainsi que les réponses traumatiques étaient influencées par l'inclinaison de l'appel-sève avant intervention. Une réduction de la tige principale réalisée sur un appel-sève dont l'inclinaison était plagiotrope a diminué la reprise de celui-ci et accru les réponses traumatiques au point de coupe.

4.2 Recommandations et perspectives de recherches futures

En règle générale, « un arbre n'a pas besoin d'être taillé. C'est l'homme qui en provoque la nécessité » (Drénou, 1999). D'un point de vue sylvicole, cette nécessité peut se traduire par l'obligation d'obtenir des troncs droits et dépourvus de nœuds (O'Hara et al., 2008; Maurin et DesRochers, 2013). D'un point de vue arboricole, au contraire, cette nécessité consiste à établir et maintenir des arbres sains, esthétiques, et sécuritaires pour le public et les infrastructures urbaines (Dujesiefken et al., 2016). Cependant, les stratégies actuelles d'intervention de taille sous les réseaux électriques n'intègrent généralement pas ou peu les connaissances connues et propres au bon développement de l'arbre (Millet et Bouchard, 2003). Dès lors, la résultante de ces interventions sur l'arbre se répercute

sur de nombreuses années sans toutefois s'atténuer dans le temps et nécessite un entretien récurrent et exhaustif sur le long terme (Goodfellow et al., 1987; Millet et Bouchard, 2003; Follett et al., 2016; Lecigne et al., 2018).

Dans une perspective d'optimisation des intervalles de retour d'entretien, tout en maintenant pour le futur des arbres sains et compatibles avec les réseaux électriques, nos différentes études ont souligné l'importance de réduire le moins possible la tige principale afin d'empêcher l'apparition de réitérations et de maximiser la compartimentation des plaies de taille (Chapitre 1), mais également pour conserver une croissance optimale de l'arbre tout en favorisant la reprise de l'appel-sève (Chapitre 3). Cet effet de la taille de réduction sur la réponse traumatique de l'arbre sera d'autant plus atténué si celle-ci est exécutée sur un appel-sève dont le diamètre est au minimum égal à un tiers de celui de la section supprimée (Gilman et Lilly, 2002 cités dans Grabosky et Gilman, 2007) et que cet appel-sève ne présente pas une inclinaison plagiotrope (Chapitre 3). Les résultats ont également mis en évidence que si une réduction de la tige principale était nécessaire pour encourager la présence et l'établissement de charpentières à une distance sécuritaire des fils électriques se trouvant à 7 m au-dessus du sol, il serait préférable de procéder à cette intervention avant que la tige principale de l'arbre ait atteint le fil, et plus particulièrement, avant ou peu après avoir atteint la zone du corridor de sécurité (Chapitre 1). Sinon, même en utilisant une intensité de taille plus faible, cette intensité éliminerait plus de 30 % de la biomasse conformément aux normes de dégagement de fil, ce qui déclencherait une initiation ainsi qu'un développement non souhaitable de réitérations. De plus, intervenir au cours de la saison de croissance permettra de limiter l'apparition et le développement de réitérations par rapport à une intervention réalisée durant la saison de dormance, sans toutefois affecter davantage la compartimentation de la plaie de taille (Chapitre 1), le développement de l'arbre, et la reprise de la dominance apicale par l'appel-sève (Chapitre 3). D'un autre côté, étant donné que les arbres les moins vigoureux produisent moins de réitérations au point de coupe (Chapitre 2), notre étude

suggère de procéder à une évaluation de la vigueur des arbres avant l'intervention de taille afin d'identifier les arbres moins vigoureux pour optimiser le temps de retour de la prochaine intervention. Finalement, pour limiter la formation de cavités au point de coupe à la suite des épisodes de taille, et donc assurer une plus grande résistance mécanique, notre étude suggère de favoriser la plantation d'espèces à compartimentation plus efficace sous les réseaux électriques (Chapitre 2).

Dans une perspective continue d'acquisition de connaissances et d'optimisation des intervalles de retour d'entretien, il paraît incontournable de développer un modèle de recroissance des arbres à la suite d'une intervention de taille pour l'ensemble du réseau de distribution électrique au Québec afin de mieux prédire et automatiser la planification des interventions de tailles. Le modèle de base pourrait essentiellement être composé de l'intensité de la taille, de la vigueur des arbres avant intervention, de l'espèce de l'arbre (Follett et al., 2016), et finalement de la saison de taille. Pour l'intensité de taille, un proxy pourrait être obtenu en fonction de la distance d'implantation de l'arbre par rapport aux réseaux électriques ainsi qu'aux types de réseaux (Millet et Bouchard, 2003) tout en intégrant le stade de développement de l'arbre (Raimbault et Tanguy, 1993). Bien que des images lidars pourraient être également utilisées pour déterminer l'intensité de taille et le stade de développement (Lecigne et al., 2018), celles-ci pourraient être couplées à des images multi/hyperspectrales pour déterminer la vigueur (Degerickx et al., 2018) et l'espèce de l'arbre (Alonzo et al., 2014). Finalement, des analyses économiques pourraient être réalisées de manière à déterminer par simulation le scénario optimal d'alternance des cycles de tailles en fonction de la saison de taille (Chapitre 1; Figure 4.1).

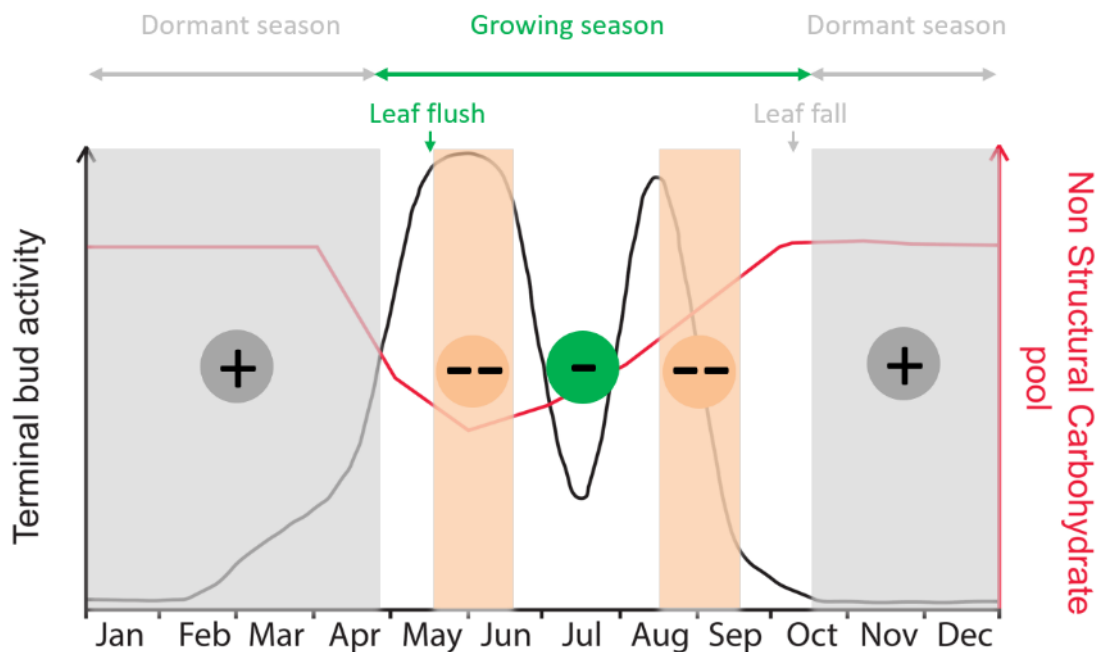


Figure 4.1 Illustration de la réponse réitérative de l'arbre à la suite d'une taille en fonction de l'activité saisonnière du bourgeon terminal (adapté de Meier et al., 2012) et des réserves (adapté de Furze et al., 2012). Une taille durant la saison de dormance (gris) est suivie par une forte réponse réitérative, alors qu'une taille durant la saison de croissance (vert) limite la réponse réitérative au point de coupe. Tailler au début du printemps ou d'automne au moment du débourrement ou juste avant la chute des feuilles (orange), respectivement, peut d'autant plus accentuer la limitation de la réponse réitérative comparativement à une taille en été.

Cette thèse s'est focalisée principalement sur l'acquisition de connaissances sur la formation des arbres se situant sous des réseaux électriques d'une hauteur de 7-8 m en réduisant la tige principale sur un appel-sève. De manière à favoriser la mise en place au point de coupe de charpentières compatibles avec les réseaux électriques tout en limitant les réponses traumatiques, une étude similaire à celle du Chapitre 3 pourrait être menée en réduisant la tige principale avec un second appel-sève initié préférentiellement du côté opposé au premier et perpendiculaire au fil (Figure 4.2). En plus de favoriser la mise en place d'une structure bilatérale en « V » à l'étape adulte, le second appel-sève pourrait limiter la production de réitérations tout en maximisant la compartimentation de la plaie au point de coupe.



Figure 4.2 Illustration du principe de réduction de la tige principale de l'arbre avec un second appel-sève localisé en face du premier et à la même hauteur (à gauche) ou légèrement plus bas (à droite). X emplacement de la tige principale réduite (adapté de Raimbault et al., 1995)

En milieu forestier, Millet et al. (1998, 1999) ont montré que les branches maîtresses (axe 2) du houppier définitif des arbres à l'étape adulte s'établissaient naturellement à des hauteurs se situant aux alentours de 10 m au-dessus du niveau du sol. En milieu ouvert, les branches maîtresses du houppier définitif s'établissent plus bas (Drénou, 2000b). Une expérience pourrait être conduite afin de démontrer la nécessité ou non d'intervenir sur la tige principale de l'arbre en la réduisant, lorsque l'arbre est implanté sous des réseaux dont la hauteur est supérieure à 9 m et de tester si la simple utilisation de tuteurs pour réorienter le développement des futures charpentières pourrait être plus bénéfique dans le processus de formation de l'arbre que d'utiliser une intervention de taille de réduction lorsque la hauteur des réseaux le permet (Millet et Bouchard, 2003; Millet, 2012, 2018).

Lorsque l'arbre n'est pas implanté directement sous les réseaux électriques, la forme de son houppier dépend principalement de sa distance d'implantation par rapport aux réseaux électriques ainsi qu'aux types de réseaux (Millet et Bouchard, 2003; Gilman, 2011; Millet, 2012). Dans ces cas de figure, des axes secondaires nécessiteront également

d'être réduits. Une étude similaire à celle du Chapitre 1 devrait être reconduite à l'échelle de la branche, de manière à démontrer la nécessité d'utiliser une faible intensité de réduction afin de n'occasionner qu'une faible réaction au point de coupe.

Au fil des années, les interventions successives de taille d'entretien sur les arbres implantés de longue date proches des réseaux électriques ont conduit pour une grande majorité des arbres à la mise en place et la prolifération de nouvelles unités réitératives sur le tronc et les charpentières maîtresses (Millet et Bouchard 2003, Follet et al., 2016). Partant du principe que plus un arbre est taillé, plus il réitère (Chapitre 1; Millet et Bouchard, 2003) et que plus on élimine les rejets, plus on engendre une accumulation de réserve au point de coupe, favorisant par la suite la repousse des réitérations au même endroit (Clair-Maczulajty et Bory, 1988; Haddad et al., 1995), il semble nécessaire de repenser la nécessité de supprimer toutes les réitérations à chaque intervention pour limiter l'intensité de taille (Millet, 2012). D'autant plus que les tailles d'entretien consistent dans bien des cas à supprimer également les réitérations se situant à une distance lointaine et nullement problématique pour les réseaux électriques. Ainsi, l'intensité de l'intervention d'entretien pourrait être diminuée en utilisant une approche de sélection des réitérations basée sur la suppression, la réduction et la conservation des réitérations en fonction de l'emplacement, de l'ancrage et de la longueur de la réitération, mais aussi sa capacité à être réduite (Figure 4.3). Ainsi, les petites réitérations proches du corridor ou les réitérations se situant à une distance lointaine, nullement problématique pour les réseaux électriques, pourraient être conservées. Les réitérations présentant un bon ancrage, mais entrant dans le corridor pourraient être réduites si et seulement si elles présentent les caractéristiques nécessaires pour être réduites. En effet, compte tenu des similitudes de développement entre les arbres individuels et les réitérations (Raimbault et Tanguy, 1993; Dujesiefken et al., 2016), des schémas similaires liés à l'intensité de la taille et à l'inclinaison de l'appel-sève pourraient affecter la production des réitérations au point de coupe après une réduction d'une réitération. Ainsi, les réitérations pourraient être réduites en utilisant les mêmes

connaissances que pour la taille de réduction de la tige principale de l'arbre. Finalement, les réitérations mal insérées (écorce incluse) ainsi que les plus longues se localisant dans le corridor, mais ne pouvant être réduites adéquatement, pourraient être supprimées. Outre le fait de diminuer l'intensité de la taille, cette approche de sélection des réitérations permettrait également de créer un écran visant à limiter la disponibilité en lumière au niveau du tronc et des branches maitresse (axe 2) dans le but de diminuer la production de nouvelles réitérations (Chapitre 1; Colin et al., 2010).

Cependant, cette nouvelle approche d'entretien des arbres adultes au contact des réseaux électriques pourrait nécessiter un temps d'intervention plus long, et donc plus onéreux. Pourtant, en augmentant la qualité de la taille, les réponses traumatiques pourraient diminuer dans le temps et, par conséquent, favoriser l'augmentation des intervalles de retour d'entretien. De nouvelles analyses économiques pourraient permettre dans un premier temps d'évaluer le temps d'entretien d'un arbre selon la méthode actuelle utilisée versus la méthode proposée et de les projeter dans le temps sur plusieurs cycles d'entretien. Dans un second temps, les analyses économiques pourraient s'intéresser aux économies réalisées lors de l'alternance des cycles d'entretien selon les saisons de taille (Chapitre 1) afin de vérifier si elles ne pourraient pas compenser l'augmentation du temps d'intervention reliée à l'utilisation d'une méthode de taille moins drastique et plus harmonieuse pour l'arbre et le ressenti des citoyens.

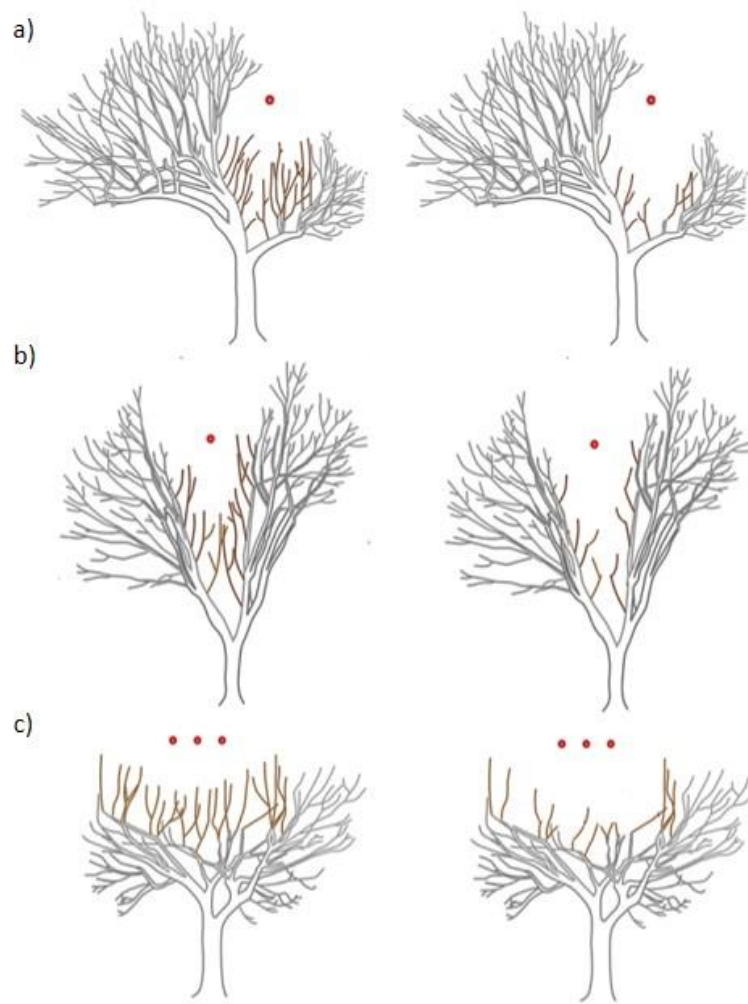


Figure 4.3 Illustration du principe de la taille de sélection des répétitions. À gauche, avant taille. À droite, après taille. (a) Arbre en forme de S. (b) En forme de V, et (c) en forme de T (adapté de Lecigne et al., 2020).

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