Université de Montréal

Facteurs écologiques régissant la régénération du chêne rouge (*Quercus rubra* L.) à la limite nordique de son aire de répartition au Québec

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Résumé

Nous avons étudié deux chênaies à la limite de l'aire de répartition de l'espèce que Québec afin de reconstruire son historique de régénération et évaluer quels facteurs gouvernent la régénération juvénile. Dans cette optique, nous avons mené une étude dendrochronologique exhaustive des chênaies et une étude sur le terrain et en serre portant sur la germination, la survie et la croissance de quatre provenances de chêne rouge (gradient nord-sud), avec ou sans herbivorie, et selon plusieurs niveaux de nutriments du sol suivant une fertilisation. Les chênaies présentent des structures d'âge similaire qui coïncident avec les dernières perturbations de feu majeures dans la région autour des années 1920. Toutefois, les chênaies diffèrent quant à la densité et la composition en espèces d'arbres, ce qui suggère des différences de régime de feu ou de statut de succession écologique antérieure au feu. Le site a eu la plus grande influence sur la régénération du chêne rouge. Les semis du site présentant la densité d'arbres, l'indice de surface foliaire (LAI) et la disponibilité en eau les plus élevés ont montré un taux de survie supérieur de 29 %. La protection contre la grande herbivorie a également affecté la performance des semis, résultant en au taux de survie supérieur de 16 % et une plus grande taille des feuilles pour trois des quatre provenances étudiées. La provenance a aussi significativement influencé la performance des semis. La provenance locale (la plus nordique) a montré la plus faible performance, avec des taux de germination, de survie et de croissance inférieures de 28 à 42 % dans les deux expériences, alors que les provenances du sud ont montré une meilleure germination et survie en serre et une meilleure survie sur le terrain. L'augmentation de la fertilité du sol s'est avérée bénéfique dans l'expérience en serre mais n'a provoqué qu'un effet marginal sur la croissance et la survie sur le terrain, suggérant que ce facteur importe moins que les autres (ex. la disponibilité en eau et en lumière) pour les stades initiaux de régénération du chêne rouge. Nos résultats suggèrent que les efforts en sylviculture visant à favoriser le chêne rouge devraient se concentrer sur la sélection rigoureuse de sites et de provenances, et que la disponibilité de l'eau peut être une condition limitante pour le succès de la régénération du chêne rouge aux stades de gland et de semis juvénile (semis de l'année) à la limite nordique de son aire de répartition.

Mots-clés : chêne rouge, régénération naturelle, facteurs écologiques, provenance, perturbation de feu, aire de répartition, migration assistée.

Abstract

We studied two red oak stands at the northern distribution limit of the species in Quebec as a means to reconstruct regeneration history and assess which factors govern early regeneration. To do so, we conducted a thorough dendrochronological study of the stands as well as germination and seedling growth experiments, both in the field and in the greenhouse, of four red oak provenances (south-north gradient), with and without large herbivory, and along various soil nutrient levels following fertilization. Stands have similar age structures with red oak establishment coinciding with the last major fire disturbance in the area in the early 1920s. However, stands differ in regard to tree species composition and density, suggesting differences in fire disturbance regime or ecological succession status prior to fire. Site had the largest influence on red oak regeneration. Seedlings at the site with the highest tree density, LAI and soil water availability exhibited a 29 % higher survival rate. Protection against large herbivory also significantly impacted red oak seedling performance, leading to a 16 % higher survival rate as well as greater leaf size for three of the four provenances studied. Germination, survival and growth also significantly differed between provenances. The local (northernmost) provenance exhibited the poorest overall performance with 28 to 42 % lower germination, survival and growth rates in the two experiments, while the two southernmost provenances exhibited superior germination and sprout survival in the greenhouse and higher survival in the field. An increase in soil nutrient availability was beneficial to red oak in the greenhouse, but only marginally benefited survival and growth in the field, suggesting that this factor is of less importance than other factors (e.g. water and light availability) for red oak early regeneration. Our findings suggest that silvicultural efforts to favor red oak should focus on site and provenance selection, and that water availability is currently limiting red oak regeneration success at acorn and early seedling life stages (i.e. yearlings) near its northern distribution limit.

Keywords: red oak, natural regeneration, ecological factors, provenance, fire disturbance, distribution area, assisted migration.

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Liste des sigles et abréviations

Provenances de chêne rouge

SBL : Station biologie des Laurentides de l'Université de Montréal

MR : Mont-Royal

PC : Pointe-au-Chêne

IA : Île-aux-Allumettes

Sites de recherche

Site 1 : Lac en Coeur

Site 2 : Lac Corriveau

Analyses statistiques

ANOVA : Analyse de variance / analysis of variance

MRT : Arbre de régression multiple / multiple regression tree

Variables

DBH : diamètre à hauteur de poitrine / diameter at breast height

LAI : Index de surface foliaire / leaf-area-index

Les hommes construisent trop de murs et pas assez de ponts.

- Isaac Newton

C'est lorsque nous croyons savoir quelque chose qu'il faut justement réfléchir un peu plus profondément.

- Frank Herbert

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Introduction générale

Mise en contexte et problématique

L'importance de la forêt pour la société se mesure à plusieurs niveaux : ressources naturelles, fonctions récréatives et services écosystémiques (Pearce, 2002). Or, les pressions appliquées sur les écosystèmes forestiers, dont l'exploitation commerciale, l'étalement urbain, la pollution (Bytnerowicz et al., 2007), l'introduction d'espèces invasives (Humble et Allen, 2006) et les transformations rapides induites par les changements climatiques (Gilliam, 2016; Ibanez et al., 2019; Weed et al., 2013) mettent en péril leur pérennité. Afin de préserver la résilience et la biodiversité des forêts, il importe donc de comprendre la dynamique de régénération des espèces d'arbres qui les composent. En ce sens, la compréhension des dynamiques de régénération est une façon d'anticiper les transformations en cours et à venir des forêts. La compréhension des dynamiques de régénération peut aussi aider à développer des méthodes afin de favoriser la régénération de certaines espèces, soient celles qui représentent d'importantes retombées économiques ou celles dont le maintien dans le paysage est davantage un problème sous les changements globaux.

Le chêne rouge nordique (*Quercus rubra* L.) est une essence d'arbre indigène d'Amérique du Nord qu'on retrouve notamment dans les forêts de feuillus et les forêts mixtes tempérées du Québec. Son aire de répartition s'étend généralement de la limite sud de la province jusqu'à la limite sud du bouclier canadien. Le chêne rouge est moins tolérant à l'ombre que les espèces de fin de succession comme l'érable à sucre (*Acer saccharum* M.) et le hêtre à grandes feuilles (*Fagus grandifolia* E.*)* (Crow, 1988; Sander, 1990). Il est donc considéré comme une espèce de début ou de milieu de succession. Son statut dans la succession écologique est sensiblement variable puisqu’il se régénère difficilement sous son propre couvert et en l’absence de perturbations de la canopée (Parker et al., 1985). Le chêne rouge s’établi préférentiellement sur des podzols avec une texture de sable limoneux ou argileux bien drainés et constitue généralement des peuplements purs ou des peuplements dans lesquels il est l’espèce dominante (Sander, 1990). Le chêne rouge présente une haute résistance au stress hydrique au stade mature ou lorsque son système racinaire est assez développé pour puiser directement dans l’eau souterraine, mais y présente une faible tolérance lors des stades juvéniles (MTESS, 2014). Le chêne rouge se retrouve donc sur une multitude de sites mésiques à xérique et de types de peuplements au sein de son aire de répartition, soit de la limite sud du bouclier Précambrien au nord jusqu’au sud des États-Unis et du Midwest nord-américain et à la côte Atlantique.

Or, depuis les années 1950, la communauté scientifique observe en Amérique du Nord un déclin généralisé de la régénération naturelle des peuplements de chênes rouges au sein de son aire de répartition (Dey et al., 2008; Loftis et McGee, 1993). Parmi les facteurs évoqués pour expliquer ce phénomène, on retrouve notamment la perturbation par le feu, la prédation, la biologie de l’espèce et la qualité du site. Au Québec, la combinaison de plusieurs facteurs dont l’exploitation pour la construction de la flotte navale au 19ème siècle, les caractéristiques écophysiologiques de l’espèce et la diminution des feux dans les forêts du sud de la province (Boulfroy, 2005) ont favorisé un éparpillement des populations de chêne rouge. Celles-ci sont désormais isolées et déclinantes et se retrouvent principalement sur des versants ou des crêtes orientées vers le sud.

Hypothèse du feu et études de brûlages dirigés

Les études paléoécologiques montrent que la prévalence du chêne rouge dans les forêts nord-américaines est associée au climat plus chaud et sec du début de l'Holocène, période durant laquelle l'incidence de perturbations par le feu était plus élevée (Abrams, 1992). Il est également avancé que les pratiques de brûlage des Premières Nations ainsi que les activités humaines liées à la colonisation européenne ont contribué à étendre l'aire de répartition antérieure de l'espèce (Dey et Guyette, 2000; Munoz et Gajewski, 2010). Toutefois, bien que cet ensemble de conditions ait favorisé la dispersion et l'établissement de peuplements matures de chêne rouge à l'échelle continentale, la régénération actuelle des peuplements de chêne rouge est plutôt caractérisée par l'établissement d'une faible quantité de semis qui ne parviennent pas ou peu à progresser vers les stades de maturité, et donc à un remplacement progressif du chêne rouge par d'autres espèces d'arbre de succession écologique plus tardive et plus tolérantes à l'ombre.

Sur le plan biologique, plusieurs adaptations spécifiques des espèces de chênes en général et du chêne rouge en particulier tendent également à favoriser cette théorie. En effet, les chênes adaptés aux sites en pente ou sur des sommets présentent des adaptations physiologiques telles que la capacité de résister aux feux, aux stress hydriques ainsi qu'à des sols relativement acides et pauvres en nutriments (Abrams, 1992). Les chênes présentent une écorce épaisse permettant aux arbres matures de résister au feu (Crow, 1988, Dey et Schweitzer, 2018), une capacité importante de produire des rejets à la suite du feu (Perala, 1974; Sander, 1990) et une certaine résistance au pourrissement suite à des blessures (Berry et Beaton, 1971; Shigo et Shortle, 1979; Brose et al., 2014). Ils sont également avantagés par l'altération des conditions du sol favorisant la germination des glands suite à une perturbation par le feu (Abrams, 1992, Greenberg et al., 2012). Pour les raisons énumérées ci-dessus et puisque le feu exerce un contrôle sur la compétition, autant sur les autres espèces d'arbres ou la végétation de sous-bois présents, on le considère grandement favorable à l'établissement du chêne rouge.

De nombreuses études de brûlage dirigé ont été menées afin de mieux caractériser l'effet du feu sur la régénération du chêne rouge. Au Massachussetts, Johnson (1974) montre que l'occurrence d'un feu printanier unique et de faible intensité peut mener à un effet antagoniste sur la régénération chêne rouge. Notamment, le feu peut favoriser une réduction du nombre total de semis ainsi qu'une diminution de leur taille en comparaison de parcelles témoin sans feu récent et/ou associées à un faible contrôle de la compétition. Toutefois, Greenler et al. (2020) ont étudié l'effet de 8 brûlages dirigés appliqués sur une période de 2 ans sur la survie et la germination de glands de chêne rouge enfouis légèrement dans l'humus. Ils ont ainsi montré une augmentation très marquée de l'émergence des semis à la suite de brûlages appliqués à l'automne et au printemps par rapport aux parcelles témoin, et une émergence des semis 1,7 fois plus élevée pour les brûlages automnaux que ceux printaniers. De façon similaire, Brose et al. (1998), ont démontré qu'une coupe progressive suivi de brûlages dirigés permet de créer des conditions favorables à la régénération du chêne rouge comparativement à des parcelles qui n'avaient pas été brûlées depuis plusieurs décennies (parcelles témoin). De plus, le type de brûlage qui est appliqué joue un rôle important dans l'évolution subséquente des peuplements. Notamment, Brose et al. (1998) ont démontré qu'un seul brûlage au printemps mais de nature sévère favorise le développement d'un peuplement dominé par le chêne rouge. En comparaison, les brûlages d'été ou d'hiver ont plutôt favorisé une régénération vers des peuplements mixtes, et ce indépendamment de la sévérité du brûlage, alors que les peuplements qui n'avaient pas été brûlés depuis longtemps ont plutôt mené à la régénération du tulipier de Virginie (*Liriodendron tulipifera* M.).

Au contraire, Granger et al. (2018) ont montré dans leur étude menée au Michigan que l'application de brûlages dirigés peut favoriser la régénération d'autres espèces que le chêne rouge, lesquelles bénéficient également des perturbations par le feu. En effet, leurs résultats suggèrent que le brûlage dirigé favorise davantage la régénération de l'érable rouge, dont l'abondance relative des tiges (toutes classes de tailles confondues) est respectivement passé de 519% à 81% dans des peuplements de chêne rouge. Knapp et al. (2015) ont étudié l'effet d'un brûlage annuel et sur un cycle de 4 ans sur la régénération dans des peuplements de chênes et de caryers spp. sur une période de 60 ans. Ils ont constaté que le traitement annuel a eu un effet limitant sur le recrutement du chêne rouge, avec une densité de 500 semis/ha en comparaison aux 4 875 semis/ha recensés pour dans les parcelles témoins. Inversement, le brûlage effectué à tous les 4 ans semble avoir grandement favorisé le recrutement du chêne rouge avec une densité observée de 14 250 semis/ha. Dans l'ensemble et indépendamment des espèces d'arbres présentes, le brûlage périodique a favorisé la production de biomasse arborée alors que le brûlage annuel a été favorable à la production de biomasse arbustive. Enfin, Knapp et al. (2015) n'ont pas noté d'effet significatif des brûlages sur la densité, la surface basale, le diamètre à hauteur de poitrine (DBH) ou la hauteur des chênes rouges adultes (DBH > 10 cm). Enfin, dans leur méta-analyse d'études portant sur les effets du brûlage dirigé sur la régénération des espèces de chênes, Brose et al. (2013) ont trouvé que les effets varient en fonction de la fréquence et de la saisonnalité du brûlage. En particulier, ils soulignent que de multiples brûlages suivis d'une perturbation de la canopée semble générer les conditions idéales pour la régénération préétablie des chênes.

Effets du feu sur les propriétés physicochimiques des sols forestiers

Outre leur effet direct sur la structure et la composition des peuplements, les feux ont également une incidence sur les conditions environnementales des forêts affectées. C'est le cas, notamment, des propriétés physicochimiques des sols. Phillips et al. (2000) ont étudié l'effet à long terme, i.e. sur une période de 35 ans, de brûlages annuels et sur un cycle de 5 ans sur la morphologie et les propriétés physiques des horizons de surfaces du sol forestier au Tennessee. Ils ont montré que l'incidence du feu provoque une diminution de la matière organique et une diminution de l'épaisseur moyenne des horizons Ah. Le sol forestier traité avec un brûlage à tous les 5 ans a conservé un mince horizon FH alors qu'une fine couche carbonisée de 1 à 2 cm s'est formée sur le sol traité avec un brûlage annuel. Les sols brûlés annuellement présentaient également une compaction accrue par rapport aux sols affectés par un brûlage aux 5 ans et les sols des parcelles témoin. En plus de détruire entièrement l'horizon FH, une occurrence annuelle du feu a eu pour effet d'augmenter la densité apparente des premiers centimètres du sol minéral.

Le feu induit également des changements au niveau chimique avec le dépôt de cendres et de charbons, sous-produits de la combustion du bois ou des végétaux qui tapissent le parterre forestier. Les cendres ont un effet alcalinisant important sur le sol, surtout par le biais d'un apport important en cations basiques contenus dans les cendres, soit le calcium (Ca), le magnésium (Mg) et le potassium (K) (Thiffault et al. 2007). Cet effet fut largement démontré par des études de fertilisation avec des cendres de bois en forêt (voir la méta-analyse de Reid et Watmough 2014). La réponse de l'humus suite à l'épandage des cendres est rapide parce que : (1) les protons sont rapidement tamponnés en contact avec les carbonates pour former les ions bicarbonates et (2) les cations basiques, notamment le calcium, sont immédiatement disponibles pour déplacer l'acidité adsorbée sur le complexe échangeable du sol (ex. H^+ et Al^{3+}). La réaction est toutefois généralement moins grande dans le sol minéral et le temps de réaction est aussi plus long parce que les cations basiques migrent plus difficilement/lentement à de plus grandes profondeurs (Lundström et al., 2003; Saarsalmi et al., 2007). L'effet tampon de la cendre varie aussi en fonction de la quantité des cendres qui parvient au sol, de la fréquence des applications et des concentrations en calcium, magnésium et potassium que les cendres contiennent. Plusieurs études ont d'ailleurs démontré un effet bénéfique de l'application de cendres de bois en tant que produit alcalinisant sur la croissance des arbres (Reid et Watmough, 2014; Emilson et al. 2020; Bélanger et al., 2021). L'application de cendres de bois a également pour effet d'augmenter le taux de minéralisation d'azote par l'ajustement à la hausse du pH du sol, ce qui favorise l'activité des microorganismes/décomposeurs (Brais et al., 2015). Toutefois, lors d'un feu, une perte en nutriments, notamment l'azote, le phosphore et le soufre, peut se faire par volatilisation (Raison 1979). La température requise pour que ce phénomène se produise dépend du nutriment. De plus, une proportion variable de la cendre produite par la combustion de biomasse végétale est soulevée par convection puis transportée sous l'effet du vent (Raison 1979). Une autre partie de la cendre déposée sur le sol est transportée par le vent et les eaux de ruissellement. De ce fait, une perte importante de nutriments peut se produire sur un site donné.

Les charbons de bois sont le sous-produit de la pyrolyse de biomasse ligneuse dans des conditions limitantes en oxygène et de température de combustion basse (Narty et Zhao, 2014). Comme les cendres, ceux-ci contribuent également à diminuer l'acidité du sol avec un apport en calcium, quoique dans une moindre mesure. L'effet tampon du charbon de bois peut toutefois fluctuer en fonction de la température de pyrolyse (Gul et al., 2015). Spécifiquement, le pH du charbon augmente généralement lorsque la température de pyrolyse est plus élevée, quoique l'amplitude de cette augmentation varie largement en fonction du type de charbon, ce qui peut faire fluctuer son effet chaulant. Les charbons de bois sont également caractérisés par une grande porosité, une haute surface de contact totale et une haute charge de surface, ce qui leur confère un effet adsorbant important. En adsorbant certains acides organiques comme les phénols sur leurs surfaces, les charbons de bois peuvent augmenter la disponibilité de l'azote en favorisant l'activité microbienne et la nitrification du sol (DeLuca et al., 2002; DeLuca et al., 2006). Le charbon peut également adsorber les composées allélopathétiques (métabolites secondaires végétaux) présents dans le sol, quoique cette capacité adsorbante peut varier en fonction du type de bois dont est issu le charbon (Keech et al., 2005; Alshahrani et Suansa, 2020). La germination des semences et la croissance des semis peuvent également être inhibées par les composés allélopathiques (Gallet et Pellissier, 2002; Reigosa et Gonzáles, 2006) et leur adsorption induit généralement une hausse de l'abondance de microbes dans le sol (Elad et al., 2011; Lehmann et al., 2011), ce qui peut contribuer à augmenter la disponibilité de certains nutriments (Jacoby et al., 2017; Zhou et al., 2020) et améliorer les conditions du sol pour certaines espèces par la neutralisation de substances phytotoxiques. Enfin, l'application de charbons de bois peut contribuer à augmenter la porosité du sol, la stabilité des agrégats, la capacité de rétention d'eau du sol, et ce de manière plus importante dans les sols à texture grossière que dans les sols à texture fine (Omondi et al., 2016). Pour ces raisons, l'utilisation de charbon comme amendement du sol en foresterie est une option (Gallet et Pellissier, 2002, Li et al., 2017), mais elle possiblement trop couteuse pour faire une application à la volée et sur de grandes surfaces.

Années semencières et provenances

Plusieurs facteurs biologiques peuvent influer sur la capacité régénérative des peuplements de chêne rouge. On note tout d'abord l'inconstance de la production de glands par les arbres matures. La production du fruit du chêne rouge suit un mode cyclique d'années semencières, c'est-à-dire que chaque année connaissant une forte production de glands est suivie de plusieurs années de faible production (voire nulle). Dans le cas du chêne rouge, ces années semencières se produisent de manière cyclique en moyenne aux 2 à 5 ans (Sander, 1990). En outre, la production de glands peut varier en fonction des individus au sein d'un peuplement et peut être augmentée par l'application d'éclaircissements sélectifs (Healy et al., 1999).

Abrams et Johnson (2013) notent l'effet significatif des années semencières sur l'établissement de semis de chêne rouge, avec une quantité initiale de 4276/ha en 2009 (année semencière) suivi de 23,000 par hectare en 2011, puis de 12,714 par hectare en 2012. Bien que les causes exactes de la production irrégulière de semences ne soient pas entièrement claires, des années caractérisées par des conditions météorologiques plus clémentes favorisaient possiblement une meilleure photosynthèse et une production fruitière plus importante ou bien que la saturation de la prédation soit en elle-même un avantage évolutif qui augmente les chances de survie des glands produits (Kelly, 1994; Sork et Bramble, 1993). Ces explications ne sont donc pas mutuellement exclusives. La production semencière représente ainsi un facteur déterminant pour la régénération du chêne rouge mais elle constitue également une source d'incertitude puisqu'elle est très irrégulière.

La taille des glands peut aussi influencer la croissance des semis de chêne rouge. Kormanick et al. (1998) ont montré une relation positive entre la masse des glands et la taille, la hauteur au collet et le taux de survie des semis. Yi et al. (2015) ont aussi montré que la masse des glands a un effet significatif sur la croissance des semis mais pas sur leur survie pour les 50 jours suivant la germination des graines, et que les plus gros glands mobilisent davantage de ressources énergétiques contenues dans les cotylédons. À l'aide d'analyses isotopiques ^{15}N, ils ont également montré que les semis issus de petits glands comportent une plus grande proportion d'azote provenant du substrat que ceux issus de glands plus volumineux, bien que cet azote ne représente tout au plus que 3% du contenu en azote dans les semis.

Sur le plan génétique, la provenance influence également la régénération du chêne rouge. Plusieurs études montrent qu'il y a une variabilité génétique entre les peuplements de chêne rouge et également au niveau interne des peuplements (Aldritch et al., 2005; Kriebel et al., 1988; Kolb et Steiner, 1989). Sork et al. (1993) ont trouvé une interaction significative entre la provenance et le site sur la résistance à l'herbivorie, estimée en fonction des dommages infligés aux feuilles de semis, ce qui tend à montrer que les chênes rouges qui composent les différents peuplements possèdent des adaptations locales. McGee (1974) a également mis en évidence un effet de l'altitude sur la phénologie de semis de chêne rouge, notamment sur le débourrement des semis et leur hauteur. Les chênes rouges provenant de sites de basses altitudes débourrent en moyenne plus tôt et connaissent une plus grande croissance verticale, tandis que l'effet significatif de site tend à supporter l'effet de conditionnement à l'altitude. Par ailleurs, Kolb et Steiner (1990) ont constaté un effet significatif des différentes provenances de chêne rouge sur la production de biomasse, et que certains génotypes semblent mieux adaptés aux conditions ensoleillées et possiblement à la compétition pour les ressources hydriques et les nutriments du sol. Au Québec, notamment, les connaissances sur l'écophysiologie des provenances de chêne rouge sont limitées et des études sont nécessaires afin d'identifier les provenances qui présentent les bagages génétiques de plus haute qualité (MacKay, 1993).

Prédation des glands et herbivorie des semis

La régénération du chêne rouge est également affectée par la prédation qui s'exerce sur les glands produits et sur les feuilles des individus à des stades juvéniles. Schnurr et al. (2004) ont montré que le recrutement du chêne rouge diminue avec l'augmentation de la densité et de l'activité des petits mammifères. Lombardo et McCarthy (2009) ont rapporté que les taux de germination sont passés de 86% à 26% lorsque les glands étaient intacts ou attaqués par le charançon (*Coleoptera : Curculionidae*). Les semis qui se sont développés à partir de glands infectés présentaient également une tige plus courte et mince, moins de feuilles, des racines plus fines et une biomasse sèche inférieure aux semis qui se sont développés à partir de glands sains. Bartlow et al. (2018) montrent toutefois que la germination de glands et la croissance de semis est possible malgré des dommages substantiels aux cotylédons, soit même lorsque > 50 % de la masse de ceux-ci est retirée. Une relation inverse significative a été observée entre la quantité de dommages subis par les glands et la croissance des semis de chêne rouge. De plus, les glands sains montraient un taux équivalent ou supérieur de germination.

Blossey et al. (2019) ont également démontré l'effet significatif de l'herbivorie du cerf de virginie (*Odocoileus virginianus*) sur les semis de chêne rouge dans l'État de New York. Ils ont trouvé une corrélation positive et significative (R^2 = 0.96) entre la population de cerfs et la proportion de semis de chêne rouge broutés annuellement, avec un taux de broutage fluctuant entre 30 % et 60 %, tout dépendamment de la population de cerf lors des années recensées. Leur étude illustre également que l'effet du broutage est d'autant plus marqué puisque plus de 60 % des semis non-protégés ont été broutés annuellement et que la croissance des semis non-protégés était inférieure à celle des semis protégés. Ward et al. (1999) ont mené une étude d'une durée de 7 ans dans des parcelles présentant une densité moyenne à élevée de cerfs (18-21 par km^2) afin de caractériser l'effet du type de protection sur la survie et la croissance de semis de chêne rouge. Ils ont montré que les semis protégés par des abris étaient 80 % plus grands que ceux protégés par des filets de mailles en plastiques, des manchons d'étoffes ou ceux sans aucune protection.

Disponibilité des ressources

La vitalité des plantes est reliée à la qualité des sites et des ressources disponibles, dont la lumière, l'eau et les nutriments, et même l'espace (sol) disponible pour le développement des racines (Messier et al. 2009). De ce fait, plusieurs caractéristiques environnementales peuvent induire des effets positifs ou négatifs dans le cas du chêne rouge. Dans leur étude menée en Pennsylvanie, Demchik et Sharpe (2000) ont montré un lien entre une déficience foliaire en calcium et potassium, ainsi qu'un plus faible rapport Ca/Al et une concentration en aluminium échangeable plus élevés dans les horizons A et B des parcelles caractérisées par de plus hauts taux de mortalité des chênes rouges matures. Kolb et al. (1990) ont montré un effet significatif de la disponibilité des nutriments et de l'eau du sol, ainsi que du niveau de lumière sur la croissance de semis de chêne rouge. Les semis de chêne rouge ont mieux performé que le tulipier de Virginie (biomasse entre 38 et 126 % supérieure dans le cas du chêne rouge) lorsqu'au moins une ressource était limitée. Inversement, le tulipier présentait une biomasse supérieure au chêne rouge (36 %) lorsque les ressources pour la croissance étaient optimales, ce qui suggère que le chêne rouge est mieux adapté à des conditions restrictives. L'étude de Phares (1971) suggère que la hauteur des semis de chêne rouge augmente de manière optimale avec 30% de la lumière disponible, alors que les semis sous 100 % de la lumière disponible produisent la plus grande biomasse. Il a été également constaté dans cette étude qu'une fertilisation équilibrée en azote, phosphore et potassium n'a pas d'effet avec seulement 10 % de la lumière disponible, mais l'effet était positif et significatif lorsque la lumière n'était pas limitante (≥ 30 %). Bauweraerts et al. (2013) ont montré que la croissance de semis de chêne rouge est significativement affectée par la température, l'humidité du sol et la concentration ambiante de CO_2. Ils ont également montré que les vagues de chaleur mènent à une production de biomasse inférieure qu'une hausse plus faible mais constante de la température, et que le stress hydrique provoque une baisse significative de la photosynthèse nette et de la biomasse produite alors qu'une augmentation du CO_2 ambiant provoque plutôt une hausse de la photosynthèse nette.

Le cas du chêne rouge en Europe

Si la régénération du chêne rouge en Amérique du Nord est fortement associée aux perturbations par le feu, ces dernières ne permettent pas d'expliquer le succès que connait l'espèce en Europe depuis son importation au 18ème siècle où les feux de forêt sont beaucoup plus rares. De ce fait, il faut considérer la possibilité que les conditions propices à la régénération de l'espèce puissent se manifester en l'absence de feu. En Europe, les sites aux sols pauvres, sableux et acides ainsi que les sites riches en argiles sont les plus propices à l'établissement du chêne rouge (Nicolescu et al., 2020). Au contraire, le chêne rouge ne s'installe pas sur les sites calcaires. Sur les sites les plus propices à son établissement, le chêne rouge montre un avantage par rapport aux autres espèces de chêne indigène qu'on y retrouve, par exemple le chêne pédonculé (*Quercus robur* L.) et le chêne sessile (*Quercus petraea*). Les besoins nutritionnels du chêne rouge, notamment en N, P et K, sont inférieurs aux autres espèces de chêne, et il présente une plus grande tolérance à l'ombre au stade de semi en raison de sa photosynthèse plus efficiente (Kuehne et al., 2014). Ce dernier avantage semble renforcé par l'application de coupes sélectives périodiques (Major et al., 2013). Nicolescu et al. (2020) rapportent que le chêne rouge est fréquemment brouté par les cervidés ainsi que les plus petits animaux tels que les lièvres, lapins ou souris. Toutefois, ils rapportent également que les glands de chênes indigènes leur sont préférés, ce qui donne un avantage supplémentaire au chêne rouge pour son établissement.

Le chêne rouge transforme l'environnement qu'il colonise. Stanek et al. (2020) ont trouvé sous couvert de chêne rouge en Pologne un appauvrissement de la plupart des nutriments et des composés phénoliques dans le sol minéral, mais également une diminution du P et des tannins dans l'humus. Bonifacio et al. (2015) ont aussi étudié l'effet du chêne rouge sur le sol dans le nord-ouest de l'Italie. Ils ont démontré qu'il altère la chimie du sol, notamment parce qu'il produit un humus plus riche en tannins et contenant des formes de carbone plus récalcitrantes par rapport à ceux produits par les chênes indigènes. Dans l'ensemble, le chêne rouge produit donc une litière de moindre qualité et moins décomposable par rapport aux espèces locales, augmente le ratio C/N et diminue la disponibilité de N, P, Ca et K, et favorise ainsi une barrière physico-chimique à l'interface du sol minéral. Enfin, en Lituanie, Riepšas et Straigytė (2008) ont observé que le chêne rouge s'établi préférentiellement sur des sites aux sols pauvres et acides, et qu'il provoque une diminution de 34 % des micromycètes, 20 % des microorganismes nitrificateurs et de 5% des microorganismes ammonisants. Il affecte aussi négativement la biodiversité locale en restreignant la présence de 11 espèces herbacées indigènes. Ainsi, puisqu'il est compétitif envers les espèces indigènes, qu'il altère les propriétés physiques, chimiques et structurelles du sol et qu'il produit des impacts indirects par l'interaction avec les autres espèces présentes, le chêne rouge est considéré comme une espèce à haut potentiel invasif en Europe (Riepšas et Straigytė, 2008; Langmaier et Lapin, 2020).

Objectifs et hypothèses de la présente recherche

Considérant l'ensemble des facteurs énumérés ci-dessus, il apparait difficile d'appréhender de façon générale le phénomène de régénération du chêne rouge à moins d'établir un plan expérimental qui permet d'intégrer l'ensemble des facteurs théoriques mis en cause. En d'autres mots, il est nécessaire de tester l'effet cumulatif de plusieurs facteurs déterminants pour bien prédire le succès ou l'échec de la régénération à une échelle géographique donnée. Les études sur le chêne rouge étant encore peu nombreuses au Québec, nous connaissons très peu les facteurs qui régissent l'établissement et la croissance de l'espèce. Dans ce sens, la recherche présentée dans ce mémoire visait à tester un nombre restreint de facteurs. Spécifiquement, nous avons mis en évidence la relation entre la régénération du chêne rouge et l'effet singulier et combiné de différents facteurs : les conditions générales de croissance du site, la provenance des glands, l'herbivorie et le niveau de fertilité du sol.

Il faut aussi noter que cette recherche sur la dynamique du chêne rouge s'est tenue à la Station de biologie des Laurentides (SBL) à St-Hippolyte, laquelle se situe à la limite nordique de l'aire de répartition du chêne rouge. Deux chênaies y ont été sélectionnées comme sites de recherche pour étudier la dynamique de régénération naturelle du chêne rouge. Ces sites sont considérés exceptionnels car les peuplements dominés par des chênes rouges matures et de grande taille sont particulièrement rares à cette latitude. Puisque l'aire de répartition du chêne rouge devrait s'étendre au nord sous l'effet des changements climatiques (Iverson et al., 2019; Prasad et al., 2020), l'emplacement de ces sites est particulièrement intéressant car il représente bien l'environnement que l'espèce pourra potentiellement coloniser au cours du 21ème siècle. En vertu de l'importance que peut revêtir le chêne rouge, tant au niveau économique comme source de bois d'œuvre ou de chauffage de qualité (MTESS, 2014) qu'au plan écologique [ex. de par ses effets sur la biodiversité par ses apports nutritifs (glands, feuilles) pour la faune (Van Dersal, 1940; Sork et al., 1983; Pekins et Mautz, 1988) ou la création d'abris (canopée) pour plusieurs espèces animales (Carey et Gill, 1980)], il est important d'explorer le potentiel de la régénération du chêne rouge à sa limite nordique afin de mieux comprendre comment l'espèce pourra évoluer sous les changements climatiques. . L'emplacement de l'étude sert donc une double fonction : mettre en place un dispositif expérimental permettant de détecter des seuils (succès/échec) de régénération dans les conditions environnementales difficiles pour l'espèce et tester la viabilité de cette régénération sous certaines conditions spécifiquement contrôlées.

La présente recherche vise ainsi à répondre à deux principaux questionnements : est-il possible d'établir un lien entre les peuplements de chêne rouge de la SBL et les facteurs théoriques mis en cause pour sa régénération? est-ce que la combinaison de plusieurs facteurs permet d'expliquer le succès ou l'échec de la régénération naturelle du chêne rouge au stade juvénile à la SBL? Le cas échéant, est-il possible d'identifier les seuils au-delà desquels la régénération n'est pas possible ? Ces questions visent à répondre aux deux objectifs de l'étude : (1) identifier, parmi les facteurs testés, ceux qui ont un effet significatif, positif ou négatif, sur la régénération du chêne rouge, et (2) comprendre la dynamique de régénération de l'espèce afin de pouvoir émettre des recommandations concernant sa germination, sa survie et sa croissance au stade juvénile.

Plus précisément, une recherche portant sur la dendroécologie des deux chênaies à la SBL nous a aussi incité à vérifier les hypothèses suivantes : (1) les deux sites d'études présentent une structure d'âges similaires, et (2) la structure d'âges des deux chênaies concorde avec les dernières grandes perturbations de feu recensées dans la région. L'étude de la structure d'âge des peuplements devrait permettre de statuer si la régénération du chêne rouge à la SBL correspond aux dernières perturbations de feu recensées sur son territoire, soit au début des années 1920 (Savage, 2001).

Une recherche sur des glands de chêne rouge menée en serre nous a incité à vérifier les hypothèses suivantes: la fertilisation a un effet positif (3) et la provenance a un effet significatif (4) sur la germination, la survie et la croissance du chêne rouge. Enfin, une recherche sur des semis de chêne rouge dans les deux chênaies à la SBL nous ont incité à vérifier les hypothèses suivantes: la fertilisation a un effet positif (5), la provenance a un effet significatif (6), l'herbivorie à un effet négatif (7) et le site a un effet significatif (8) sur la survie et la croissance du chêne rouge.

Ecological factors affecting red oak (*Quercus rubra* L.) regeneration near its northern distribution limit in Québec

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Introduction

Red oak (*Quercus rubra* L.) is native of North America and is characterized by a wide distribution, ranging from the upper midwestern United States (Minnesota) to the Canadian Maritimes (Nova Scotia) to the southeastern (Mississipi) and south-central (Oklahoma) states. However, regeneration of red oak has been limited in the last century (Dey et al., 2008; Loftis et McGee, 1993). Its past regeneration was mostly attributed to the warmer and dryer climate of the early Holocene (Abrams, 1992) and could also have been favored by First Nations and European settlements (Dey and Guyette, 2000; Munoz and Gajewski, 2010). Fire disturbance is apparently needed to favor red oak regeneration (Abrams, 1992; Shumway et al., 2001; Brose et al., 2013; Brose et al., 2014). Studies on prescribed burning suggest that fire disturbance can enhance red oak regeneration, although fire frequency and severity determine red oak regeneration success or failure (Johnson, 1974; Brose et al., 1998; Knapp et al., 2015; Greenler et al., 2020). Red oak has fire-resistant physiological adaptations such as post-fire sprouting (Perala, 1974; Sander, 1990), bark thickness (Crow, 1988, Dey and Schweitzer, 2018) and wood compartmentalization after fire injury (Berry et Beaton, 1971; Shigo et Shortle, 1979; Brose et al., 2014). These adaptations lead to the idea that fire is a primary driver of red oak regeneration. The benefits of fire disturbance on red oak regeneration include the suppression of late-successional, shade tolerant competing species (Brose et al., 1998; Dey et Guyette, 2000) and soil amendments with wood ash and charcoal, but this may also benefit other species such as red maple (*Acer rubrum* L.) (Green et al., 2010; Granger, 2018).

The production of wood ash during a fire improves the acid-base status of the forest floor, e.g. pH and exchangeable Ca, Mg and K, whereas the effects of ash on the mineral soil appear several years or decade after deposition, and the amplitude of its effect varies as function of the amount of ash produced (Lundström et al., 2003; Thiffault et al., 2007; Reid et Watmough, 2014). By increasing soil pH, wood ash can also affect N mineralization, thus generating overall improved soil conditions for plant growth (Raison, 1979; Brais et al., 2015, Bélanger et al., 2021). Additionally, with its high surface area, charcoal can improve soil conditions for plant growth by adsorbing allelopathic compounds such as tannins and phenols, which are recognized as adversely impacting red oak acorn germination and seedling radicle growth (Lodhi, 1978; Hanson, 1987). This effect varies with the types and sources of allelopathic substances (Nilsen et al., 1999). Adsorption of phenols can also increase soil microbial activity and nitrification (DeLuca et al., 2002; DeLuca et al., 2006; Elad et al., 2011; Lehmann et al., 2011) and thus further improves nutrient availability (Jacoby et al., 2017; Zhou et al., 2020). However, fire can negatively impact soils by decreasing organic matter levels and increasing bulk density at the very surface (Phillips, 2000).

Other important factors affecting red oak regeneration include its 2 to 5 years masting cycle (Sander, 1990; Sork and Bramble, 1993; Abrams and Johnson, 2013), acorn predation (Schnurr et al., 2004; Lombardo and McCarthy, 2009), herbivory (Ward et al., 1999; Blossey et al., 2019), acorn size and quality, e.g. free of infections (Kormanick et al., 1998; Yi et al., 2015), genotypes which are characterized by very specific adaptations (McGee, 1974; Kriebel et al., 1988; Kold et Steiner, 1990; Sork et al., 1993; Aldritch et al., 2005) and site intrinsic conditions including soil physicochemical properties as well as light and water availability (Phares, 1971; Kolb et al., 1990; Demchik et Sharpe, 2000; Bauweraerts et al., 2013). While red oak fails to regenerate in its native distribution range, its regeneration has been very successful in Europe since its introduction in the 18th century (Marjor et al., 2013; Nicolescu et al., 2020). The fast expansion in Europe where fire disturbance is not prevalent suggests that red oak regeneration is not entirely dependent of fire disturbance, and that other factors (e.g. climate) may play a large role in its failure to regenerate in North America.

Red oak is an important tree species to maintain in the North American landscape as it is a source of high-value lumber (MTESS, 2014) and is a significant food source and shelter for fauna (Van Dersal, 1940; Carey and Gill, 1980; Sork et al., 1983; Pekins and Mautz, 1988). Models project that climate change should be beneficial to the expansion of red oak in northeastern North America and a northern shift in the distribution of the species is expected (Iverson et al., 2019; Prasad et al., 2020). However, such models are generic and they generally overlook specific conditions and environmental factors that control regeneration at finer spatial scales. As such, studies on the regeneration dynamics of red oak at its northern distribution limit is of value because a better understanding of the early ecology of the species will guide management strategies to maintain the species at these latitudes and perhaps to increase its distribution northward under climate change. We thus studied two mature red oak stands at the northern distribution limit of the species in Quebec, a rare occurrence at such latitudes. Studying red oak stands at the species' northern distribution limit has benefits in the sense that it is an environment that will likely become more prevalent for red oak under climate change. Our first objective was to measure tree density, species composition and age structure as a means to assess red oak regeneration history in the stands. We hypothesized that both stands exhibited similar age structure, fire disturbance playing a significant role in the establishment and dominance of red oak trees and thus red oak age should closely match the last fire occurrence in the early 1920s (Savage, 2001) Our second objective was to assess the influence of a series of defined factors on red oak early regeneration, i.e. site intrinsic conditions, acorn provenance, herbivory and soil fertility, by conducting germination and seedling growth experiments in a controlled environment (greenhouse) and in the two red oak stands. We hypothesized that the site intrinsic conditions and provenance would significantly affect germination, survival and growth of red oak, that large herbivory would have adverse impacts, and that increasing soil nutrient availability by adding wood ash and biochar would have a positive influence.

Materials and Methods

Study site

The study was conducted at the Station de Biologhie des Laurentides (SBL) of Université de Montréal in St. Hippolyte, Quebec (45°98′93″ North and 74°00′61″ West, Figure 1). The site is at the northern limit of the maple-yellow brich (Bertula alleghaniensis) bioclimatic domain of the lower Laurentians. It is mostly composed of maple stands in mesic sites and coniferous stands (*Abies balsamea* or *Thuja occidentalis*) in hydric and sub hydric sites (Savage, 2001). The sites is characterized by the warm-summer humid continental climate typical of southern Québec: The mean annual temperature, precipitation, days without frost and degree-days simulated with the BioSIM model (Régnière and Bolstad 1994) between 2003 and 2013 were respectively 4.9 °C, 1270 mm (with 30 % falling as snow), 153 and 2845 (Bélanger et al. 2021). Soils are sandy and developed from glacial till made up of anorthosite (Morin series) and felsic rocks (Bélanger et al. 2012). The site is part of the Grenville geological province, which is in turn part of the Canadian Precambrian Shield They are classified as Orthic Ferro-Humic and Humo-Ferric Podzols (Soil Classification Working Group 1998).

We studied the only two red oak stands at SBL. Both Lac en Coeur (site 1) and Lac Corriveau (site 2) appeared appropriate for our study because they offered diversity in terms of structure and species composition. Both stands have mature and dominant red oak trees and are situated on well-drained hilltops with south-southeast facing slope aspects. Also, their selection for the study seemed relevant given that they are near the northern distribution limit of the species and exhibit limited red oak regeneration. The study at SBL involved two components. First, we assessed stand age, tree species composition and basal area per species. Second, we conducted field experiments of acorn germination and seedling survival and growth of different red oak provenances. We collected acorns from three sites, whereas another one was acquired from the Quebec Government. We also conducted a greenhouse experiment to study germination, survival and growth of these provenances under optimal growing conditions.

Stand characterization

Four and five 452 m^2 circular plots (12 m radius) were randomly selected in SBL sites 1 and 2, respectively. Within each plot, all trees with a diameter at breast height (DBH) > 10 cm were identified by species, measured for DBH and cored using a Haglof 5.1 mm diameter increment borer.. Collected tree cores were prepared and sanded using standard methods (Payette, 2011) before counting growth rings under a Leica M80 binocular microscope. For each plot, we computed the percent contribution of each tree species to the total number of trees (abundance) and calculated basal area (m^2/ha) and mean DBH and age per species. Total basal area was also measured for each plot. We then calculated site means for all these variables as a means to describe and compare stand characteristics between both sites.

Acorn collection and stratification

Red oak acorns were collected in pristine forests at three different sites in the fall of 2017. Acorn collection sites included SBL as well as Mont-Royal (MR), Pointe-au-Chêne (PC) and Isle-aux-Allumettes (IA), all within the province of Québec. These sites are shown in Figure 1. The sites were selected to capture a latitudinal gradient which mainly encompasses differences in climate but also in geology, soils and stand compositions. The MR is situated at 45°30′23″ North and 73°35′20″ West, PC at 45°65′45″ North and 74°74′68″ West and IA at 45°51′24″ North and 77°4′0″ West. The PC site also belongs to the Grenville geological province, and its soils were developed from glacial till characterized by uncategorized gneiss and marbles (Government of Québec, 2018). The MR site is part of the Monteregian Hills complex and is characterized by a magmatic intrusion formed during the late Mesozoic (~125 Ma), unearthed by the differential erosion of the glaciers' over the last 2 million years. Thus, soils are are mostly formed from melanocratic and leucocratic gabbro (Amórteui et al., 2010). The IA is part of the Trenton group and its soils are derived from alkaline sedimentary rocks, including limestone, dolomite and shale (Thériault et al., 2012). Like SBL, the MR, PC and IA sites are characterized by the warm-summer humid continental climate typical of southern Québec, although they MR and PC are warmer and have less precipitation. The MR, PC, IA and SBL respectively present a 6.8, 6.1, 5.0 and 4.3°C mean annual temperature and 1000.3, 1008.9, 853.1 and 1192.9 mm mean annual precipitation for the 1981-2010 period (Government of Canada, 2020). Also, the MR and PC sites are respectively located in the sugar maple-bitternut hickory and at the intersection of the sugar maple-basswood and sugar maple-yellow bioclimatic domains (Saucier et al., 2009).

Acorn stratification was completed following the protocol described by Nature-Action Québec (2015). The acorns were first washed with a diluted NaClO solution (5 %) of the original concentrated bleach solution (3 %). This allowed to kill pathogens and/or mold, thus maximizing the conservation of seeds from the start-to-end of the stratification process throughout the winter period. Acorns were then selected based on the criterion of non-viable vs. viable acorns. More specifically, acorns that presented visible outside damages (mold, fissures, holes, etc.) were discarded as non-viable. Also, acorns that floated during the bleaching process were assumed to have an affected core (e.g. weevil, *Curculo glandium* M.) and were thus also discarded (Figure 2). Sorting of the acorns was done to allow optimal quality and germination rates.

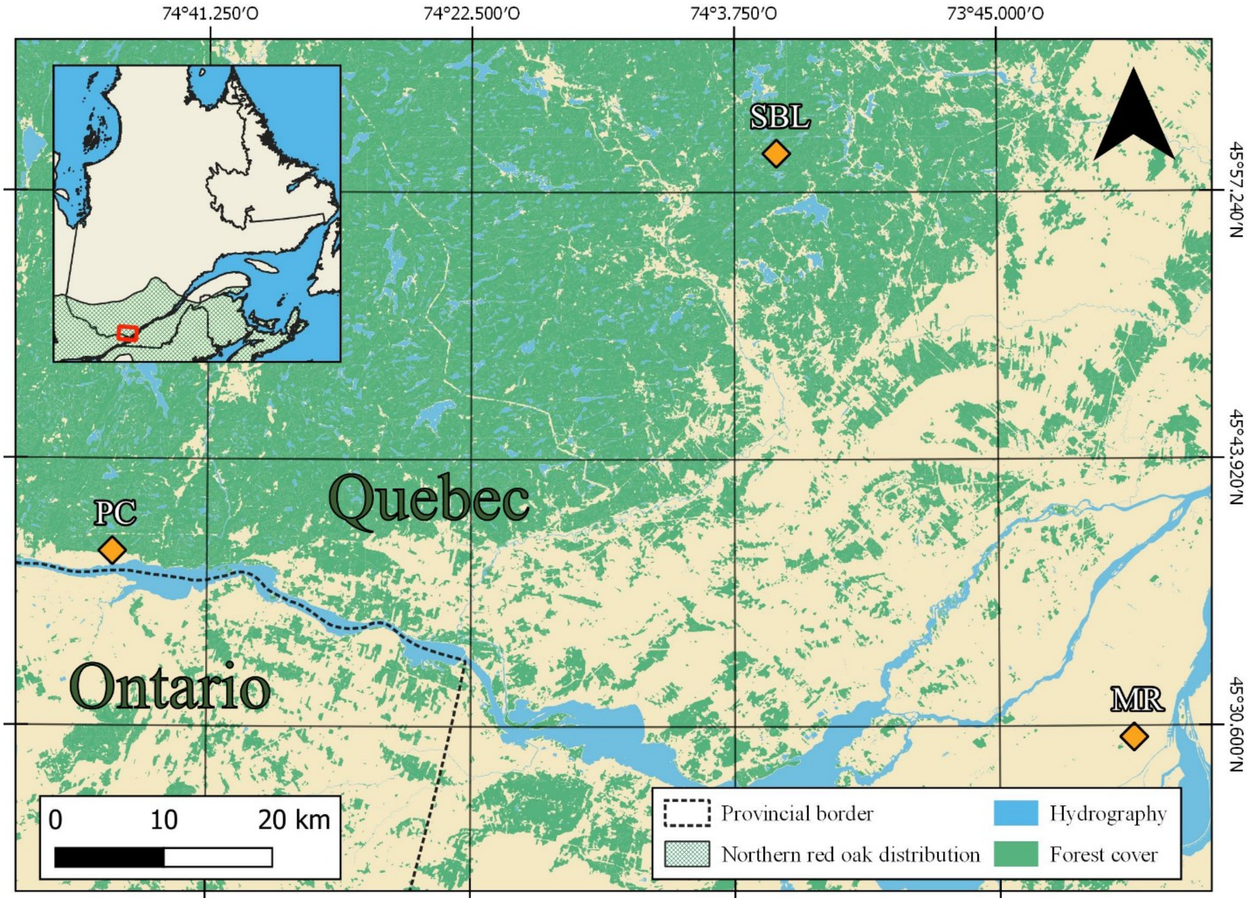

Figure 1. Site locations of red oak acorn provenances used in the experiments. Data was gathered from Gouvernement du Québec (2021) and map projection is NAD Quebec Albers (EPSG:6624).

Acorns were stored in the refrigerator at 2° C for three months in large Ziplock™ bags prepared with a vermiculite bed to absorb the excess initial moisture. Distilled water was then sprayed in each bag on a weekly basis to maintain relative humidity at about 25 % to prevent drying. Bags were also opened each week to oxygenate acorns and prevent mold development. Finally, acorns were soaked in water for 24 hours one day prior to transplantation in the pots or field plots.

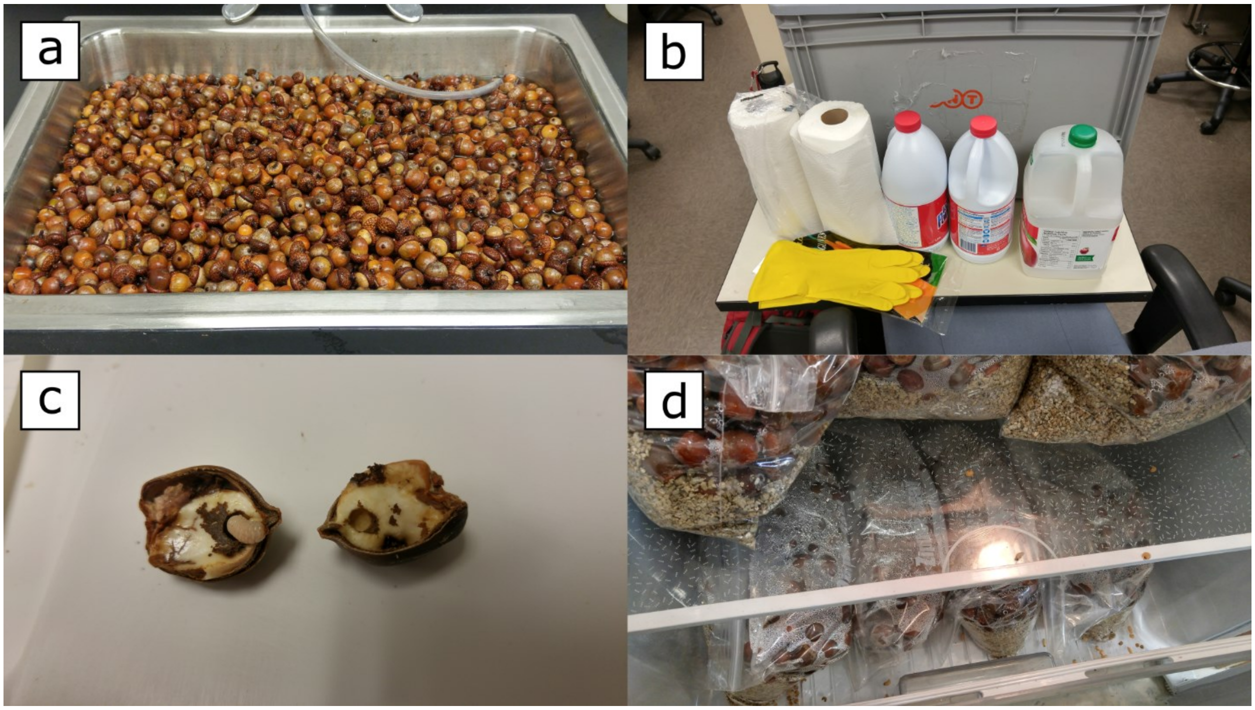

Figure 2. Some images of the acorn stratification process. Acorns were washed in a diluted bleach solution (a and b). The presence of acorn weevil (Curculo glandium) was prevalent in the collected samples (c). Many were found digging their way out of the acorns and plastics bags during storage in the refrigerator during stratification (d).

Greenhouse experiment

A first experiment was carried out in the greenhouse with the objective of characterizing germination rates, growth and survival of the red oak provenances under a soil richness gradient. This experiment was conducted during summer 2018 in a greenhouse located at the Université du Québec à Montréal (UQÀM). One acorn was planted at the soil surface in 100 cm^3 pot. A total of 170 acorns were planted for SBL and 230 acorns were planted for MR and PC each. The pots were placed in 21 rows containing 30 pots each (Figures 3 and 4). Each row was comprised of three sets of 10 pots of each provenance, placed randomly along the rows. Soil richness treatments were randomly distributed along the rows in sets of three pots. This ensured that both the provenances and treatments were distributed throughout the room, which reduces possible bias induced by unaccounted environmental variations in the greenhouse.

The potting soils were prepared from a base of sand mixed with a rich organic soil (Agro Mix® N7). The soil richness treatments were produced from mixing the sand and organic soils in varying proportions. The sand and organic soil mixture corresponded to 9:1, 5:5 and 1:9 ratio for the low, average and high soil richness treatments, respectively. The sand and organic soil mixtures were prepared in a concrete mixer, which we ran for 10 minutes to obtain a fully homogenized soil. Salifu and Jacobs (2006) studied red oak seedling growth under different fertilization treatments and showed that a fertilization of 15N-15P-15K of 25 mg N plant^{-1} season^{-1} maximized dry mass production, 100 mg N plant^{-1} season^{-1} led to optimum N and P uptake, and 150 mg N plant^{-1} season^{-1} induced N and P toxicities. Based on this information, we applied a water soluble 20N-20P-20K fertilizer (Miracle-Gro™) to the pots to enhance differences between the soil richness treatments. The low soil richness treatment received a total 3.75 mg N of fertilizer season^{-1}, while the average soil richness treatment received 15 mg N season^{-1} and the high soil richness treatment received 75 mg N season^{-1}. Equivalents using a 15N-15P-15K fertilizer would be 5 mg, 20 mg, and 100 mg N for the low, average and high soil richness treatments, respectively.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
	T3	T2	T1	T3	T2	T1	T2	T1	T3	T1	T2	T3	T1	T3	T2	T3	T2	T1	T3	T1	T2
Rows 1 to 10	B	A	C	A	B	A	A	C	C	B	B	A	A	B	C	C	B	C	C*	B	C
Rows 11 to 20	A	B	B	C	A	B	C	B	A	C	C	B	B	C	A	A	C	B	C	B*	B*
Rows 21 to 30	C	C	A	B	C	C	B	A	B	A	A	C	C	A	B	B	C*	A	B	C	B

Figure 3. Full layout of the greenhouse experiment. There are 21 rows (from A to U), each associated with a specific soil richness treatment (low (T1), average (T2) and high (T3)). In each row, 10 acorns from each provenance were planted in 30 pots (i.e. one acorn per pot).

Air temperature was set at 24 °C during the day and 20 °C at night, whereas light was provided for 16 hours d^{-1}. These parameters were monitored/controlled by a centralized system. Pots were watered using a tubing system with individual outlets planted in each pot. The watering system was activated two times per week for a duration of 1 minute (equivalent to 300 ml of water per pot). This kept the soil evenly moist but not saturated. Excess water could easily drain as the bottom of the pots was perforated.

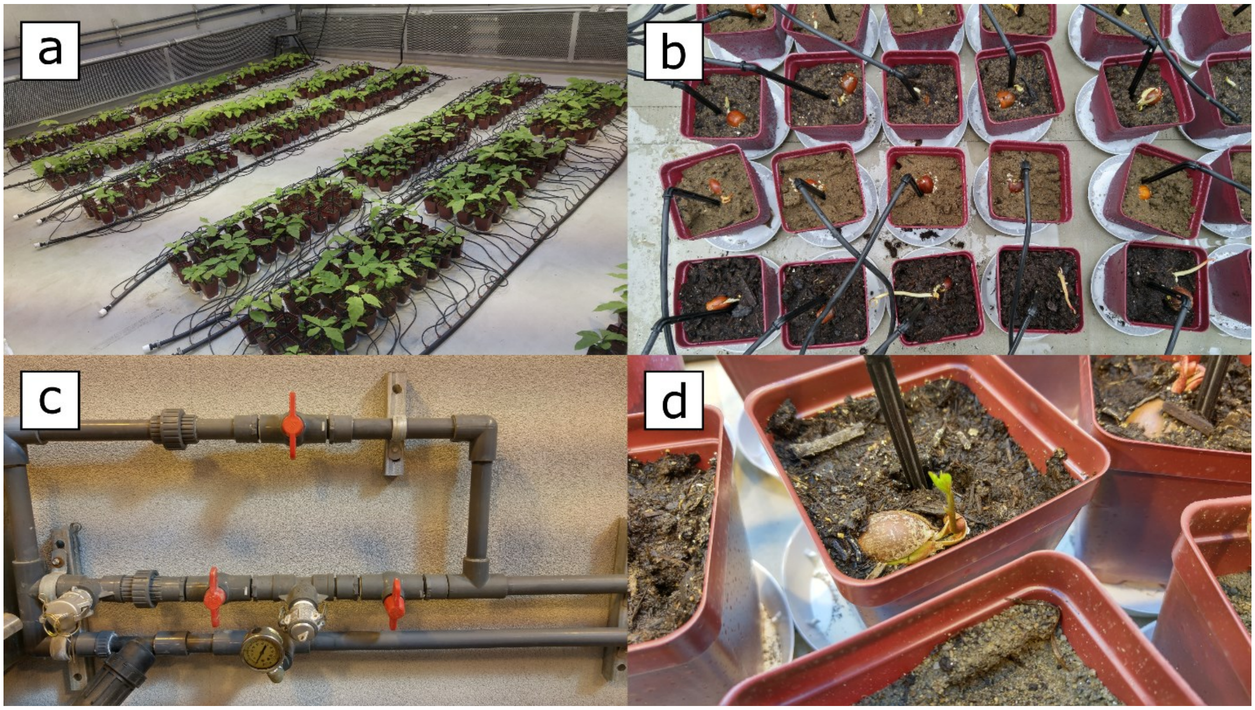

Figure 4. Some images of the greenhouse experiment, including the full layout with soil richness treatments aligned in rows along the red arrow (rows A to U) and 30 pots per row, 10 for each provenance, one acorn per pot, along the green arrow (a). The watering system can be seen running within the buffer areas. The three soil richness treatments can be observed, the lighter one being the low soil richness treatment, the darker one being the high richness treatment, and the other one being the average soil richness treatment (b). The valve/water used to water the pots with an equal quantity distributed to each pot (c). Acorns were planted at the soil surface in order to emulate germination in the natural environment (d).

To assess the performance of red oak provenances as a function of soil richness, growth stage levels were measured throughout the experiment. Stage 1 corresponded to a successful germination, stage 2 corresponded to stem development, stage 3 corresponded to the onset of leaf development, and stage 4 corresponded to multiple/full leaf development. Germination and sprout survival rates were also monitored. We also calculated a total mortality rates per provenance, which corresponded to the number of dead sprouts as well as the seeds that did not germinate. A subsample of seedlings (*n* = 32, 40 and 36 for SBL, MR and PC respectively) was selected at end of the experiment for destructive measurements. Response variables measured were stem height (cm), stem mass (g), number of leaves, leaf mass (g), leaf surface area (cm^2), support root mass (g) and fine root mass (g). Leaf area (cm^2) was assessed for the greenhouse subsample seedlings, by scanning leaves as .tiff files on a white paper sheet as background and then estimating leaf area with the LeafArea R package, which acts as an interface for the image processing program 'ImageJ'. All mass measurements were carried out on dried samples (40 C for 48 h), whereas leaf surface area was measured on flat-air dried leaves. Other variables derived from direct measurements were mean leaf mass (g $leaf^{-1}$), mean leaf foliar surface (cm^2 $leaf^{-1}$), aboveground biomass (g), belowground biomass (g), total biomass (g) and root:shoot mass ration.

Potting soils from the three soil richness treatments were sampled at the beginning and end of the experiment (i.e. weeks 0 and 10). Soils collected at the onset and end of the experiment were representative of substrates without and with the weekly addition of a fertilizer. Three replicates were sampled for each treatment, for a total of 18 soil samples. These samples were then brought to the laboratory for chemical analysis.

Field experiment

A second experiment was carried out in the field at SBL. The experiment design included ten blocks distributed evenly among Lac en Coeur and Lac Corriveau (Figure 5). Each block contained twenty-four 900 cm² micro-plots separated by 10 cm wide buffers (Figure 6). Micro-plots were identified with stake flags. Half of the micro-plots were set up within a 6 feet high galvanized metal fence in order to protect red oak seedlings from large herbivory (e.g. deer) (Figure 7). The other half of the micro-plots was left unprotected from large herbivory. Each half-block was subdivided randomly into 3 provenances and 4 soil fertilization treatments. The layout was randomly distributed based on the protection of large herbivory (factor 1), followed by the soil fertilization treatments (factor 2), and finally by the random distribution of the 3 provenances within a soil fertilization treatment (factor 3). The soil fertilization treatments included a control, wood ash, biochar, and a combination of ash and biochar. In the fall of 2017, wood ash and biochar were applied at the soil surface at a rate of 1 Mg (dry) ha^{-1}, i.e. the lowest rate at which plant growth (maize) was observed (Glaser et al. 2015) and at which the acid-base status of the soil was significantly (positively) affected (Brais et al. 2015). It is thus believed to be a very conservative application rate for both materials, whereas the combination of wood ash and biochar was used as a means to emulate the effect of forest fires on soils. Leaf litter was removed before applying the material and then placed back. Wood ash came from the Domtar pulp and paper mill in Windsor and has a water content of 40 %, a pH of approximately 12.3 and a neutralizing capacity of 52 % (Domtar, personal communication), whereas the biochar was prepared from coarsely grinding wood charcoal prepared from eastern hardwoods using a leaf grinder. Wood ash was sieved at 2 mm before being applied, whereas biochar was applied without sieving (Figure 7). Although Fertilization was done prior to the next growing season for the soil to react before red oak acorns were planted. Twelve acorns per micro-plot were planted in the first 5 cm of forest floor during the last week of May 2018. Again, to do so, leaf litter was removed and placed back.

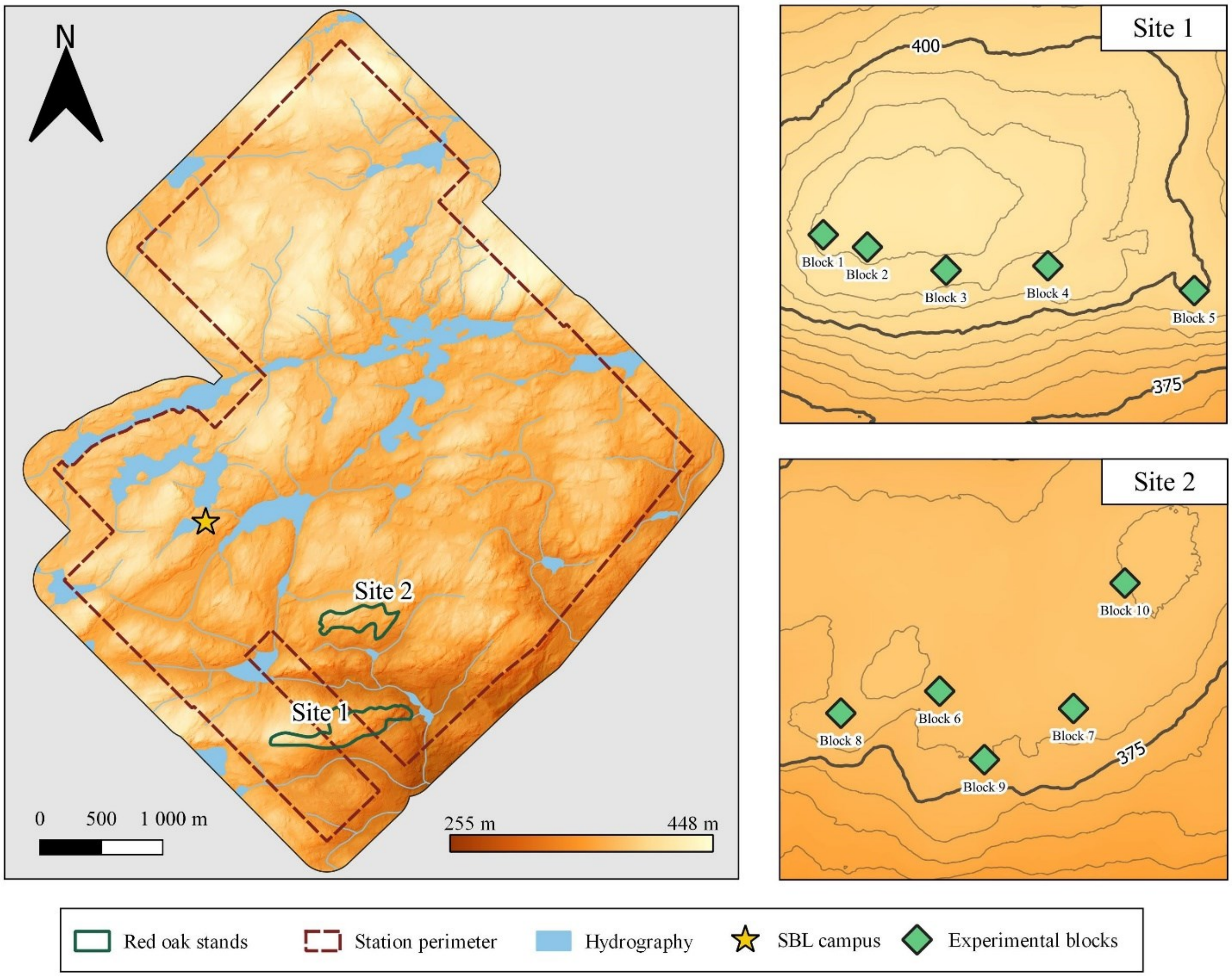

Figure 5. Map of the experimental blocks at SBL study sites. Data was gathered from Gouvernement du Québec (2021) and map projection is NAD83 MTM 8 (EPSG:2950).

This first attempt resulted in total death of planted acorns after a two-week period. Indeed, heavy rodent predation (mainly eastern chipmunk, *Tamias striatus*) and very dry conditions proved fatal for all planted red oak acorns. A new experiment was thus conducted using the seedlings grown in the greenhouse. The saplings were first placed in dormancy in the fall by progressively reducing photoperiod and temperatures in the greenhouse. As a whole, seedlings had four months of growth. These were later transferred and buried under snow in early December 2018 at SBL.

Micro-plots were re-fertilized at the same rate prior to the snow. The saplings were then transplanted in the micro-plots in June of 2019. Unfortunately, because of a malfunction of the watering system, a significant number of saplings died after the 10-weeks experiment and consequently, a smaller number of saplings were transplanted. To compensate this loss, a new provenance, Île-aux-Allumettes (IA), was added to the experiment. This material was obtained from the *Ministère des forêts, de la faune et des parcs* of the Quebec Government. The acorns were stratified at UQAM from December 2018 through April 2019 (as described in the previous sections), germinated in pots on the SBL campus area in May 2019 and then transplanted on the sites in June 2019. However, the seedlings were transplanted 2 weeks after the others due to delays in getting them ready. They were transplanted when acorn predation was no longer a concern for seedling survival. Three SBL, four MTL, and five PC and IA provenances were transplanted in the micro-plot. In the end, the 3 original provenances were planted in one block in site 1 (block 3) and one block in site 2 (block 6), for a total of 48 plots (16 micro-plots per provenance) and 48 SBL seedlings, 64 MTR seedlings and 80 PC seedlings, whereas the IA seedlings were planted in two blocks in site 1 (blocks 2 and 4) and two blocks in site 2 (blocks 7 and 9), for a total of 32 plots and 160 seedlings.

We assessed the effect of provenances and soil fertilization treatments on germination, survival and growth rates following a schedule with decreasing frequency (from 2 times a week, to once a week and to twice in august). We also monitored herbivory from any signs of browsing damage and activity/movement of small animals within the blocks using cameras equipped with sensitive motion detection sensors (see Figure 7). Measured response variables were survival (%), growth stage, number of leaves and foliar surface (cm^2). Seedling survival was visually estimated with the presence/absence of leaves and buds and the stem dryness level. Growth stage was estimated based on the size of the largest leaf of the seedling, ranging from 1 to 5 cm^2 (e.g. stage 5 corresponded to the largest leaf at 5 cm^2). Number of leaves and total leaf area of each seedling were estimated only once in mid-July. Leaf size was assessed using the same template used for the greenhouse experiment. Other response variables derived from data were longevity (i.e. number of weeks alive), mean leaf surface area (cm^2 $leaf^{-1}$) maximum growth stage, final growth stage and growth stage regression (i.e. difference between maximum and final growth stages).

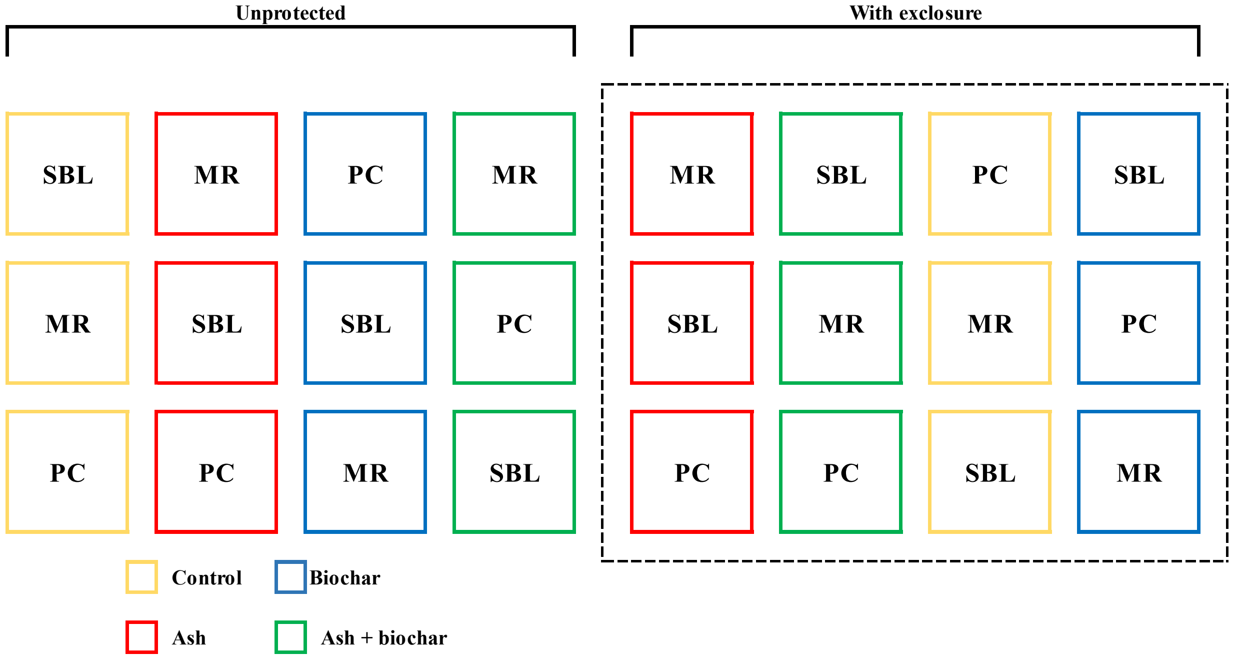

Figure 6. Example of an experimental field block with three nested factors. Each block was divided in two parts, one unprotected and the other protected by a fence, i.e. exclosure (first factor). Each side was then subdivided into four soil fertilization treatments (second factor). Each provenance (SBL, MR and PC) was then distributed within each soil fertilization treatment (third factor). All factors were randomly distributed. Individual plots were separated by 10 cm buffers to avoid contamination between soil fertilization treatments.

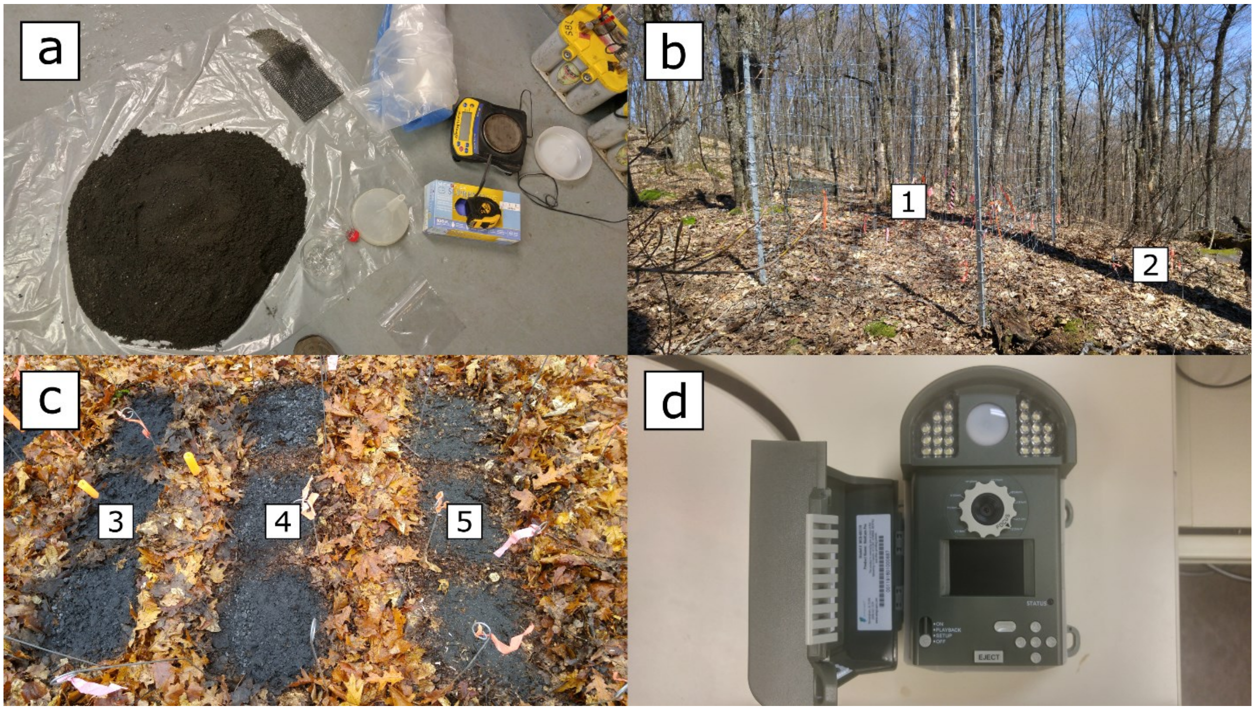

Figure 7. Some images of the field experiment. Wood ash from the Domtar pulp and paper mill in Windsor was sieved at 2mm (a). Six feet high galvanized metal fences were used to build exclosures (b). 1 is for protected micro-plots and 2 is for unprotected micro-plots. The micro-plots were fertilized with biochar (3), a combination of ash and biochar (4) and ash (5) once leaf litter was removed (c). Leaf litter was placed back after fertilization. The control micro-plots are not shown. A high-resolution bird-watching camera equipped with an adjustable-sensitivity motion detection senso (Wingscapes Birdcam Pro, Moultrie) was used to capture close-range images of day and night animal activity/movement withn the blocks (d).

Other environmental variables were also measured in the experimental blocks in order to better characterize growing conditions during the study period. Soil temperature was measured using type-K thermocouples that were manufactured in our laboratory. Six thermocouples were placed within each block (3 in the unprotected area and 3 in the exclosures) at a 12 cm depth within the buffers. Temperature was recorded using a thermocouple digital thermometer (Treacable®, Cole-Palmer). Soil volumetric water content was measured with time-domain reflectrometry using a FieldScout TDR 300 Soil Moisture Meter (Spectrum technologies) equipped with 12.2 cm probe. Measurements were repeated 3 times around each thermocouple. Leaf area index (LAI) was measured during full canopy July to characterize the light environment within each block using a CI-110 Plant Canopy Imager (CID Bio-Science). Measurements were conducted at 1.5 meters above the soil surface.

Since we did not want to disturb the soil where acorns and seedlings were planted, side plots with and without fertilization were established as a means to sample soils, i.e. forest floor and upper podzolic B horizon, and thus assess the effects of ash and biochar on soil chemical composition. These side plots were established as one pair of the control, wood ash, biochar and wood ash+biochar treatments beside each experimental block. Forest floor upper podzolic B samples were collected from each treatment, for a total of 8 soil samples in each block or 80 samples in total.

Soil analysis

Soil samples were quickly brought back to the laboratory where they were immediately dried in an oven at 50 °C over a full week. A portion of the dried samples was used for measuring pH and exchangeable Ca, Mg, K and P, whereas the rest was ground to < 60 μm (PM 400 Planetary Ball Mill, Retsch) for analyzing the bulk chemical composition, including total C and N. Soil pH in water was measured using soil:water ratio of 1:10 for the forest floor and 1:5 for the mineral soil (Hendershot et al., 2007). Exchangeable Ca, Mg, K and P were measured following a Mehlich 3 extraction (Ziadi and Tran, 2007). Calcium, Mg and K concentrations were measured by atomic absorption spectroscopy (55 AA analyzer, Agilent Technologies), whereas P concentrations were measured using the molybdenum blue colorimetric method (SmartChem 200 Discrete Analyzer, AMS Alliance). Total C and N concentrations were measured by combustion at 1040 °C and infrared and thermal conductivity detection, respectively (EA 1108 CHNS-O Elemental Analyzer, Thermo Fisons). Ground samples were also pressed in pellets (13 mm diameter × 10 mm thickness) using a 25 tons hydraulic press (Reflex Instruments). Bulk chemical composition was assessed by X-ray fluorescence spectrometer (Vanta M series, Olympus) equipped with a rhodium tube of 50 kV and a silica drift detector. For upper podzolic B samples, we report results using the Geochem calibration mode, with one built-in beam filter operating at 40 kV for heavier elements and another operating at 10 kV for lighter elements. Scanning time was set to 30 s per beam such that one whole scan was completed in 60 s. Analyzer drift was verified every 25 pellets with a silica blank. For forest floor samples, we used the same analytical conditions. However, to minimize matrix effects relative to using typical X-ray fluorescence standards with a dominant inorganic component, five customized Ca, Mg, K, Al and P standards made of cellulose, lignin, xylose and gallic acid to emulate the chemical proportions of cellulose (32%), lignin (28%), hemi-cellulose (25%) and tannins (15%) forming organic soils were used for data calibration. The linear relationship between P concentrations of the standards was highly significant ($R^2 = 0.98$ to 0.99 for Ca, Mg, Al and P, and $R^2 = 0.92$ for K).

For the greenhouse experiment, we used Plant Root Simulator (PRS) probes (Western Ag Innovations, Canada) to assess solution ionic activity of the different soil richness levels. To do so, we followed a paste preparation protocol which was then placed on the probes for 3 hours (Quian et al., 2008). Four pairs of cation and anion probes were prepared for each soil richness level. The paste was then removed and the probes were cleaned with deionised H_2O and stored in the fridge in zipseal bags until analysis. Elution of the probes was done for 1 h with 0.5 M HCl. NH_4-N and NO_3-N were determined colorimetrically by continuous flow analysis (Autoanalyser III, Bran & Luebbe, USA), whereas other ions ($H_2PO_4^-$, Ca^{2+}, Mg^{2+}, K^+, Al^{3+}, Fe^{3+} and Mn^{2+}) were determined by inductively coupled plasma atomic emission spectroscopy (Optima 3000-DV, PerkinElmer, USA).

Statistical analysis

Parametric analysis of variance (ANOVA) tests and multiple regression trees (MRT) were used to test the effects of various factors on response variables. For the field experiment, response variables were converted into percent values due to unbalanced number of individuals between plots. For the greenhouse experiment, parametric ANOVAs and permutational ANOVAs were used to categorize the effects. of provenances and soil richness. For the field experiment, ANOVAs were used on the four nested factor levels, i.e. site, protection from large herbivory (with or without exclosures), soil fertilization and provenances. In the ANOVA, both provenance and soil richness/fertilization were used as the fixed factors. A Tukey post-hoc test was used to identify factor level differences at an alpha significance threshold of 0.05 for the greenhouse experiment and 0.1 for the field experiment. In the latter case, a higher alpha level was preferred because of the low number of denominator degrees of freedom. We proceeded in this manner by keeping in mind that the consequence of failing to detect a difference which did occur in nature (type II error), which is necessarily bound to the alpha level, is likely more serious than the consequence of detecting a difference which did not occur (type I error) (Peterman 1990). When the conditions of independence of the observations, normality of the residuals and homoscedasticity were not met, data were transformed with square root or natural logarithm.

Multivariate regression trees (MRT) are used to produce graphical representations of the relationship between selected response variables and explanatory factors. In ecology, MRT are used to describe and predict relationships between species data and environmental parameters

(De'ath, 2002). In this research, the specific MRT approach used is the conditional inference trees variant, which is a 'non-parametric class of regression trees embedding tree-structured regression models into a well-defined theory of conditional inference procedures' (Hothorn et al., 2006). The MRT are produced by the *ctree* function within the *party* package (Hothorn et al., 2006) in the R environment (R Core Team, 2019). Other R packages used to compute results or produce graphical representations include *dplyr* (Wickham et al., 2020), *ggplot2* (Wickham, 2016), *gridExtra* (Auguie, 2017), *multcomp* (Hothorn et al., 2008) and *splines* (R core team, 2019).

Results

Tree species composition, age structure and biomass

Both sites are characterized by the dominance of red oak and sugar maple. The tree species composition in site 1 is less diversified than site 2. In site 1, red oak and sugar maple have an identical relative abundance and make up for 92.8 % of the sampled trees, whereas only 3 other species were inventoried (Table 1). Site 2 exhibits a more diversified composition as 11 species were inventoried in the stand. Red oak and sugar maple also make up for the bulk of the trees in site 2 (i.e. relative abundance of 89 %), but in contrast to site 1, red oak is substantially less abundant than sugar maple. Tree density is higher at site 2 than site 1, with an average of 566 and 382 trees per hectare, respectively (results not shown). This difference in density is also reflected by the LAI measurements taken. Values averaged 1.9 and 2.4 at sites 1 and 2 respectively. Red oak, sugar maple and American beech are the only three tree species present in both sites. All other tree species identified are present only at site 1 or at site 2.

Red oak and sugar maple were the oldest tree species at both sites (Table 2). One *Fraxinus nigra* M. tree was the exception in site 1, with a similar age (90 years) to the red oak. Many *Fraxinus nigra* trees were found near the south edge of site 1 (at a lower position on the hillslope) and the old *Fraxinus nigra* tree may thus originate from another stand with a different disturbance history and composition that borders the southern limit of site 1. Our results suggests that red oak trees in site 1 established sooner than sugar maple trees by an average of 18 years. Conversely, red oak trees at site 2 are on average 7 years younger than sugar maple trees. Red oak is the dominant species at site 2 and exhibits a basal area and a DBH that are respectively 2.5- and 1.6-fold the basal area and DBH of sugar maple. As a whole, our results suggests that red oak is relatively close in age to sugar maple, and perhaps older as in site 1, but our data do not account for possible sugar maple seedling.

Table 1. Tree species frequencies and relative abundances in the two study sites. The abbreviations presented here are used in Table 2.

Species	**Abbreviation**	**Frequency**		**Abundance (%)**	
		Site 1	**Site 2**	**Site 1**	**Site 2**
Red oak (*Quercus rubra*)	RO	32	29	46.4	22.7
Sugar maple (*Acer saccharum*)	SM	32	60	46.4	46.9
American beech (*Fagus grandifolia*)	ABe	1	5	1.5	3.9
White spruce (*Picea glauca*)	WS	-	6	-	4.7
Balsam Fir (*Abies balsamea*)	BF	-	9	-	7
White birch (*Betula papyrifera*)	WB	-	10	-	7.8
American basswood (*Tilia americana*)	AB	-	3	-	2.3
Red maple (*Acer rubrum*)	RM	-	2	-	1.6
Striped maple (*Acer pensylvanicum*)	StM	-	2	-	1.6
Eastern cottonwood (*Populus deltoides*)	EC	-	1	-	0.8
Yellow birch (*Betula alleghaniensis*)	YB	-	1	-	0.8
American hophornbeam (*Ostrya virginiana*)	AH	3	-	4.3	-
Black ash (*Fraxinus nigra*)	BA	1	-	1.4	-

Table 2. Diameter at breast height (DBH), average age and basal area of the various tree species present in sites 1 and 2. Values are means ± standard errors. Total basal area is 59.15 and 34.81 m2/ha for sites 1 and 2 respectively.

Species	**DBH (cm)**		**Tree age (years)**		**Basal Area (m^2/ha)**	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
RO	54.7 ± 7.9	37.9 ± 2.2	95.2 ± 2.9	79 ± 4.6	41.79	16.29
SM	32.6 ± 5.9	23.1 ± 0.8	78.3 ± 5	86.2 ± 2.6	16.47	11.78
Abe	9.5	18.7 ± 1.4	25	68.2 ± 11.1	0.04	0.62
WS	-	21.8 ± 3.1	-	62.1 ± 4.7	-	1.38
BF	-	17.3 ± 0.8	-	63.2 ± 7.2	-	1.29
WB	-	27.2 ± 1.2	-	77.8 ± 4.9	-	2.88
Aba	-	16.8	-	72.5	-	0.31
StM	-	18.4	-	43	-	0.26
AH	14.7	-	58.5	-	0.35	-
BA	34	-	90	-	0.50	-

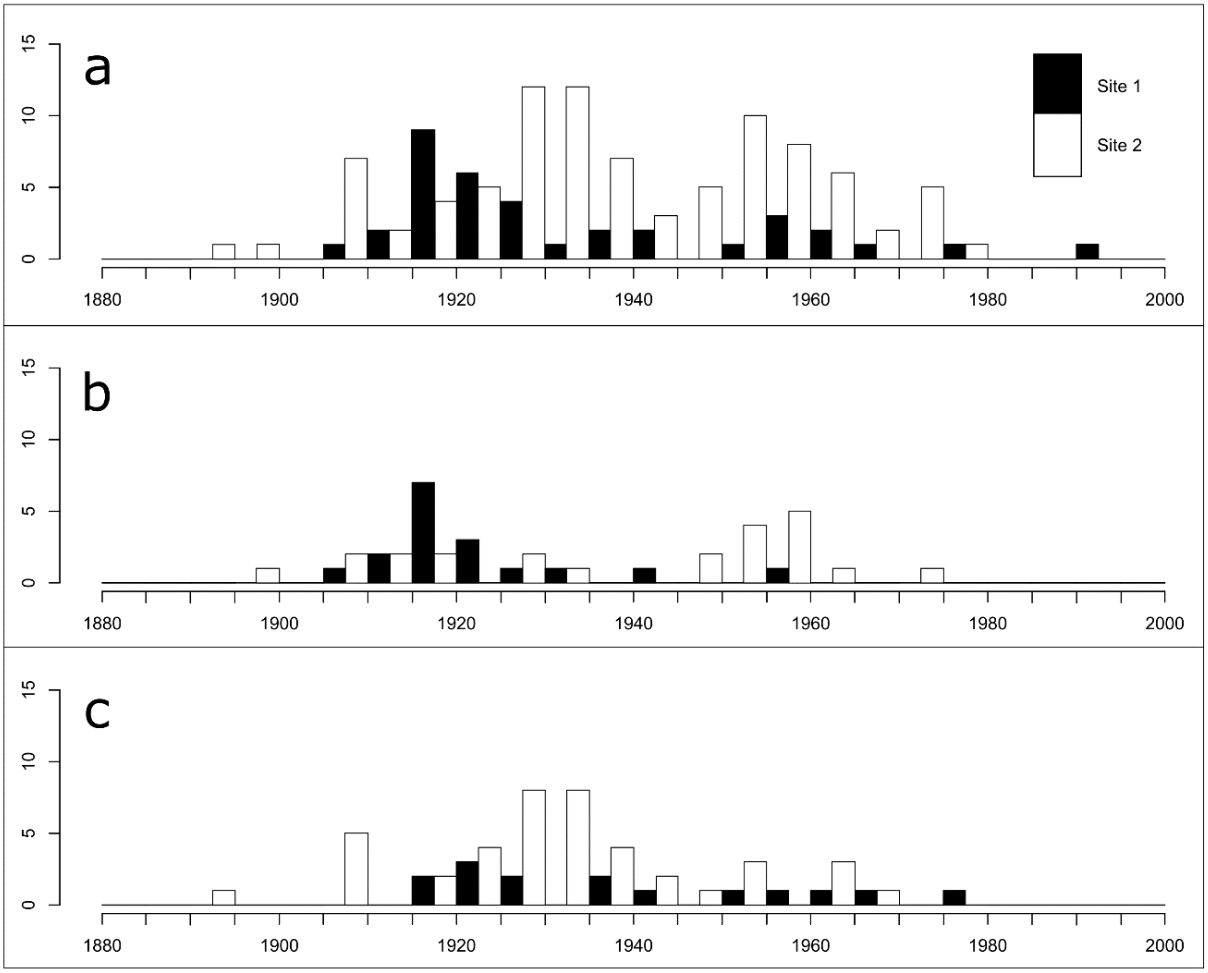

Figure 8. Age structure of (a) all cored trees, (b) red oak and (c) sugar maple at the two study sites.

Note: Data are only accounting trees for which growth rings could be counted in whole. Trees with rotten or empty cores are not accounted for. For tree species with less than 5 stems, no standard error was calculated.

Red oak and sugar maple trees have an average DBH of 54.7 cm and 32.6 cm in site 1 and of 37.9 cm and 23.1 cm at site 2, respectively. Due to some uncertainties of tree age, the faster growth of red oak compared to sugar maple is difficult to confirm with DBH data only. However, growth rings were also generally wider for red oak. The base diameter of trees, measured at 30 cm from the soil surface, also suggest a size advantage of red oak. Basal area difference between red oak and sugar maple at sites 1 and 2 were about 25 and 5 m^2/ha, respectively. Many red oak trees showed fused stems within the first 100 cm, which is characteristic of a post-fire regeneration pattern, i.e., multiple stems growing from the same stool. Fire scars on these main bases were often visible, but they were not investigated further to assess the year of fire occurrence more precisely.

A more in depth look at the age structure of the stands (Figure 8) provides an insight of the regeneration dynamics at both sites. First, very few trees were older than 1906. At that point in time, there was a substantial increase in tree recruitment rates at both sites. Tree recruitment at site 1 mainly occurred during two periods, i.e., 1910 to 1924 and 1951 to 1965. At site 2, recruitment dynamics were not as well defined in time. Recruitment rates were highly variable between 1907 and 1980, shifting from high to low, and they were nearly zero thereafter. Red oak recruitment occurred mainly between 1910 and 1933 at site 1, with a record year in 1918. Sugar maple recruitment was high between 1918 and 1930 and it was irregular and more largely spaced in time between 1930 and 1978. No more recruitment of sugar maple occurred thereafter at site 1. There was steady but small recruitment of red oak at site 2 between 1900 and 1931, whereas high recruitment occurred between 1947 and 1960. Sugar maple recruitment at site 2 mostly occurred between 1907 and 1947. Recruitment of sugar maple was negligible thereafter and completely absent from 1970 and onward.

Greenhouse experiment

Ionic activities of the soil substrates as measured by paste extracts on PRS probes confirm a strong increase in the availability of macronutients for red oak seedlings from the low to average to high soil richness treatments (Table 3). The only exception was for NH_4-N which suggest relatively homogneous supply rates between the 3 treatments

Table 3. Availability of macronutrients under the 3 soil richness treatments using paste extracts on PRS probes of soils collected at the end of the 10 weeks greenhouse experiment.

Ion	Treatment ion supply (µg/10 cm²)		
	Low	Medium	High
Total N	8.20	13.5	22.9
NO_3-N	3.46	5.96	16.7
NH_4-N	4.74	7.50	6.14
Ca	103	419	799
Mg	19.5	72.9	131
K	35.0	239	525
P	0.41	1.63	8.12
S	31.6	121	180

Germination rates of all red oak provenances increased with soil richness (Table 4). An overall increase of about 12% from the low soil to the rich soil richness treatments. However, red oak provenances displayed variation in germination rates in the following order: SBL < MR < PC. Seedling sprout survival rates of all red oak provenances were highest under average soil richness and lowest under low soil richness (Table 4). Sprout survival rates were similar between SBL and MR, whereas PC showed higher values.

Table 4. Germination, sprout survival and total mortality rates of red oak as a function of soil richness and acorn provenance over 10 weeks of greenhouse experimentation.

Response variable	Soil richness			Acorn provenance		
	Low	Average	High	SBL	MR	PC
Germination	61.2%	65.2%	73.7%	43.2%	71.7%	85.1%
Sprout survival	84.5%	96%	90%	87.6%	88.7%	94%
Total mortality	48.3%	37.4%	33.7%	62.2%	36.4%	20%

On the one hand, the MR and PC provenances showed an increase in germination rates with increasing soil richness (Table 5). On the other hand, the SBL provenance exhibited the greatest germination rate under low soil richness (i.e. 50 %), which was a lower germination rates than those observed for the MR and PC provenances under low soil richness. The total mortality rate for the SBL provenance was highest under high soil richness, whereas mortality rates for the MR and PC provenances were highest under low soil richness and lowest under high soil richness. The only provenance that did not suffer post-germination mortality up to the 10th week of experiment was PC within the average treatment (Table 5). The MR provenance also displayed the largest differences in germination, sprout survival and total mortality rates between the low and high soil richness treatments.

The multivariate regression tree (MRT) analysis on germination rates suggests a first partition within the provenance factor, with the SBL provenance being separated from the MR and PC provenances (Figure 9). A second partition is suggested within the treatment factor for the MR and PC provenances, with the low soil richness treatment being separated from the average and high soil richness treatments. A third partition separates the MR provenance from the PC provenance, whereas a final partition separates the average soil richness treatment from the high soil richness treatment for the MR provenance (Figure 9).

Table 5. Germination, sprout survival and total mortality rates of red oak provenances as a function of soil richness over 10 weeks of greenhouse experimentation.

Factor level		Response variable					
Acorn prov.	**Soil richness**	***n***	**Germination**	***n***	**Sprout survival**	***n***	**Total mortality**
SBL	Low	60	50%	30	93.3%	60	53.4%
	Average	50	38%	19	89.5%	50	66%
	High	60	41.7%	25	80%	60	66.6%
MR	Low	70	60%	42	73.8%	70	55.7%
	Average	80	70%	56	98.2%	80	31.3%
	High	80	85%	68	94.1%	80	20%
PC	Low	80	73.6%	59	86.4%	80	36.4%
	Average	80	87.5%	70	100%	80	12.5%
	High	70	94.3%	66	95.5%	70	9.9%

Morphological variables are presented in Table 6. As a whole, the high soil richness was associated with higher height, foliar surface and leaf, stem and root masses, whereas the low soil richness treatment exhibited the lowest values. The average soil richness treatment did exhibit slightly higher stem mass than the high soil richness treatment. Root/shoot ratio was about 0.8 under low and average soil richness, while the ration was about 0.7 under high soil richness.

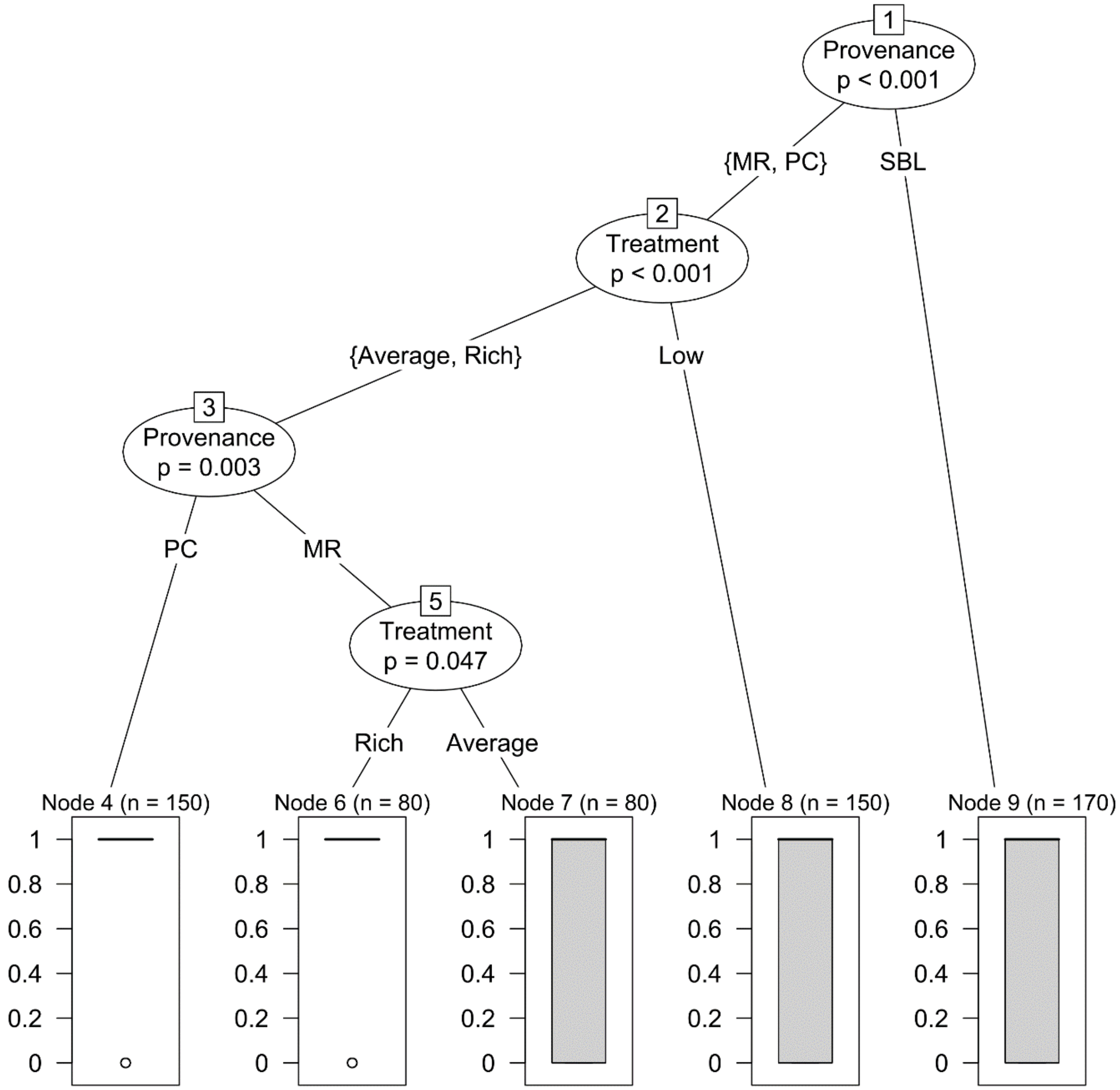

Figure 9. Multiple regression tree of red oak germination rates (as a yes/no binary variable) as function of soil richness and acorn provenance over 10 weeks of greenhouse experimentation.

Table 6. Morphometric variables measured on red oak seedlings as a function of soil richness and acorn provenance at the end of the 10 weeks greenhouse experiment. Values are means ± standard errors.

Response variable	**All seedlings (n=108)**	**Soil richness treatment**			**Provenance**		
		Low (n=45)	**Average (n=46)**	**High (n=17)**	**SBL (n=32)**	**MR (n=40)**	**PC (n=36)**
Stem height (cm)	7.47 ± 0.28	7.17 ± 0.31	7.65 ± 0.24	7.79 ± 0.30	6.16 ± 0.22^{a}	7.77 ± 0.30^{ab}	8.30 ± 0.28^{b}
Number of leaves	5.59 ± 0.24	5.11 ± 0.21	5.97 ± 0.25	5.88 ± 0.29	5.19 ± 0.15	5.70 ± 0.32	5.83 ± 0.21
Total leaf area (cm^2)	118 ± 6.12	93.5 ± 4.61^{a}	128 ± 5.96^{b}	154 ± 7.78^{b}	92.0 ± 4.59^{a}	139 ± 7.89^{b}	117 ± 4.00^{ab}
Mean leaf area (cm^2)	22.9 ± 1.24	19.9 ± 1.04^{a}	23.2 ± 1.13^{ab}	29.9 ± 1.73^{b}	19.3 ± 1.06^{a}	26.4 ± 1.51^{b}	22.1 ± 0.96^{ab}
Leaf mass (g)	0.74 ± 0.04	0.57 ± 0.03^{a}	0.81 ± 0.04^{b}	0.98 ± 0.05^{b}	0.57 ± 0.03	0.86 ± 0.05	0.75 ± 0.03
Mean leaf mass (g)	0.14 ± 0.01	0.12 ± 0.01^{a}	0.15 ± 0.01^{ab}	0.20 ± 0.01^{b}	0.12 ± 0.01^{a}	0.16 ± 0.01^{b}	0.14 ± 0.01^{ab}
Stem mass (g)	0.24 ± 0.01	0.18 ± 0.01^{a}	0.29 ± 0.02^{b}	0.27 ± 0.02^{ab}	0.18 ± 0.01^{a}	0.29 ± 0.02^{b}	0.25 ± 0.01^{ab}
Support roots mass (g)	0.57 ± 0.03	0.43 ± 0.02^{a}	0.67 ± 0.02^{b}	0.71 ± 0.04^{b}	0.48 ± 0.03^{a}	0.57 ± 0.03^{ab}	0.66 ± 0.03^{b}
Fine roots mass (g)	0.111 ± 0.006	0.114 ± 0.007	0.114 ± 0.004	0.100 ± 0.007	0.104 ± 0.007	0.111 ± 0.005	0.119 ± 0.005
Aerial biomass (g)	0.99 ± 0.05	0.77 ± 0.03^{a}	1.10 ± 0.05^{b}	1.27 ± 0.07^{b}	0.76 ± 0.04^{a}	1.16 ± 0.06^{b}	1.01 ± 0.03^{b}
Root biomass (g)	0.69 ± 0.03	0.54 ± 0.02^{a}	0.78 ± 0.03^{b}	0.81 ± 0.05^{b}	0.58 ± 0.03^{a}	0.68 ± 0.03^{ab}	0.78 ± 0.03^{b}
Total biomass (g)	1.68 ± 0.07	1.31 ± 0.05^{a}	1.88 ± 0.07^{b}	2.08 ± 0.10^{b}	1.34 ± 0.06^{a}	1.84 ± 0.09^{b}	1.79 ± 0.05^{b}
Root / shoot	0.79 ± 0.04	0.80 ± 0.04	0.81 ± 0.03	0.70 ± 0.04	0.84 ± 0.04	0.70 ± 0.04	0.84 ± 0.04
Fine roots / support roots	0.23 ± 0.01	0.29 ± 0.02^{a}	0.19 ± 0.01^{b}	0.16 ± 0.01^{b}	0.24 ± 0.02	0.24 ± 0.01	0.20 ± 0.01
Fine roots / leaves	0.19 ± 0.02	0.24 ± 0.02^{a}	0.17 ± 0.01^{a}	0.11 ± 0.01^{b}	0.20 ± 0.01	0.20 ± 0.02	0.17 ± 0.01

Table 7. Two-way parametric and permutational ANOVA test results on morphometric variables measured on red oak seedlings as a function of soil richness and provenance at the end of the 10 weeks greenhouse experiment (see Table 6). Values in with * indicate a significant effect at P<0.05. Most of the variables that have significant P values for either soil richness treatments or acorn provenances also show a significant interaction term between the two factors, which suggests that response variables may behave differently depending on the combination of factors.

Response variable	**Parametric 2-way ANOVA**					**Permutational ANOVA (n=5000)**		
	Transf.	**Shapiro**	**Treatments**	**Provenance**	**Interaction**	**Treatments**	**Provenance**	**Interaction**
Stem height	√	0.928	0.45	0.004*	0.25	0.67	0.001*	0.34
Number of leaves	log	0.005	-	-	-	0.24	0.68	0.16
Total leaf area	√	0.608	2.1e-04*	4.7e-03*	3.8e-04*	8.6e-04*	7.3e-06*	1.1e-04*
Mean leaf area	log	0.279	0.059	0.073	0.013*	0.039*	0.002*	0.008*
Leaf mass	√	0.662	7.2e-05*	3.6e-03*	9.2e-05*	2.4e-04*	5.6e-06*	4.4e-05*
Mean leaf mass	log	0.287	0.05	0.09	0.006*	0.017*	0.002*	0.003*
Stem mass	√	0.739	3.0e-04*	0.002*	0.025*	9.0e-04*	4.1e-04*	0.017*
Support roots mass	√	0.730	6.4e-05*	0.019*	0.29	1.4e-05*	0.005*	0.11
Fine roots mass	√	0.047	-	-	-	0.53	0.25	0.14
Aerial biomass	√	0.183	3.3e-05*	5.3e-04*	1.1e-04*	1.3e-04*	1.8e-06*	7.0e-05*
Root biomass		0.511	7.3e-05*	0.017*	0.065	1.6e-04*	0.005*	0.065
Total biomass	√	0.813	6.4e-06*	0.001*	6.5e-04*	1.1e-05*	8.2e-06*	3.2e-04*
Root / shoot	√	0.504	0.38	0.19	0.096	0.70	0.26	0.13
Fine roots / support roots	log	0.255	1.9e-04*	0.54	0.26	2.0e-04*	0.62	0.35
Fine roots / leaves	log	0.323	1.8e-04*	0.54	0.31	0.005*	0.82	0.50

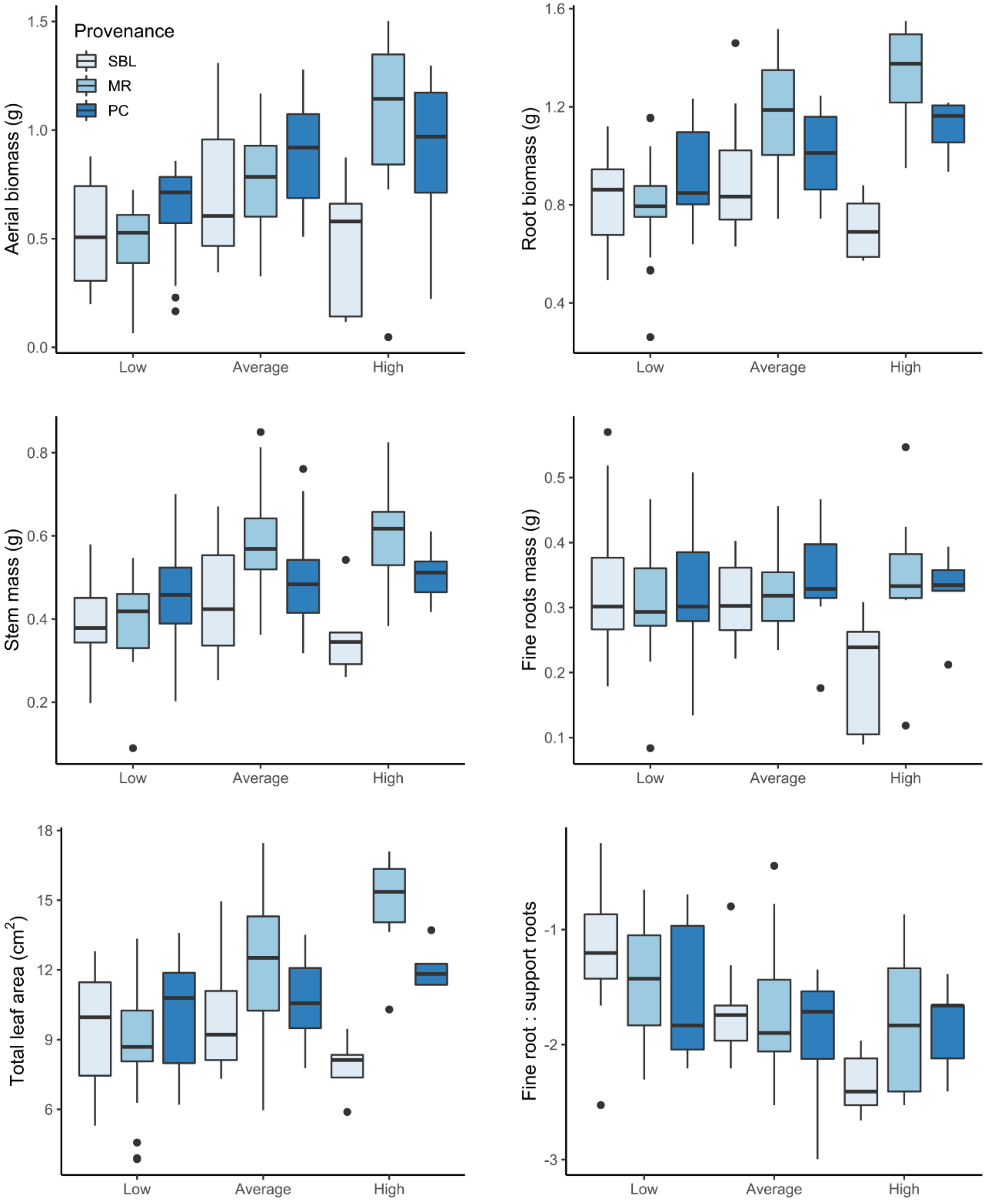

Figure 10. Boxplots of normalized response variables measured in the greenhouse experiment (see table 6 for transformation used).

Two-way parametric and permutational ANOVA tests suggest that total leaf area and mass as well as stem mass were significantly different between soil richness treatments, between provenances, and that there was a significant interaction between the two factors (Table 7). Boxplot analysis of these variables (figure 10) indicate that this interaction is the result of the SBL provenance. While performance of the MR and PC provenances generally increased with soil richness, the SBL provenance performed at its maximum under average soil richness and performance substantially decreased under high soil richness. ANOVA tests also suggest a significant difference in stem height between provenances, in support root mass between soil richness treatments and between provenances, and in ratio of fine roots mass/support roots mass and fine roots mass/leaf mass between treatments.

Field experiment

Chemical analyses show that forest floor composition is generally similar between the sites (Table 8). However, site 1 has higher mineral soil total C and N concentrations as well as higher extractible Ca, Mg and K concentrations, whereas soil pH is lower. Ash and biochar fertilization treatments had a substantial increasing effect on forest floor Ca, Mg and K concentrations and pH but had no detectable effect on the mineral soil. As expected, forest floor pH was lowest in control plots, while ash led to a substantial increase in pH and Ca, Mg and K concentrations. Biochar only slightly increased forest floor pH and Ca, Mg and K, whereas the combination of ash and biochar showed the largest increase (Table 8).

Table 8. Forest floor (FH) and mineral soil (B) chemical properties as a function of site and fertilization treatments at SBL. pH is pH in water, C and N is total carbon and nitrogen, and calcium (Ca), magnesium (Mg) and potassium (K) concentrations are from a Mehlich-3 extraction.

Soil samples		pH	C	N	Ca	Mg	K
			%		cmol(+) kg^{-1}		
Organic (FH)	Site 1	4.61 ± 0.08	30.2 ± 5.10	1.49 ± 0.18	13.9 ± 2.81	2.68 ± 0.62	0.80 ± 0.16
	Site 2	4.72 ± 0.18	32.3 ± 4.08	1.45 ± 0.16	12.7 ± 6.35	3.16 ± 1.16	1.64 ± 0.37
	Control	4.67 ± 0.09	-	-	13.3 ± 3.12	2.92 ± 0.60	1.22 ± 0.26
	Ash	5.24 ± 0.13	-	-	31.6 ± 5.18	5.81 ± 0.66	2.01 ± 0.29
	Biochar	4.85 ± 0.15	-	-	18.5 ± 3.36	3.60 ± 0.60	1.56 ± 0.14
	Ash+biochar	5.87 ± 0.19	-	-	37.1 ± 1.91	6.35 ± 0.55	1.95 ± 0.30
Mineral (B)	Site 1	5.00 ± 0.13	8.46 ± 1.18	0.42 ± 0.03	1.97 ± 1.16	0.34 ± 0.17	0.13 ± 0.04
	Site 2	5.29 ± 0.10	5.87 ± 0.66	0.27 ± 0.03	0.36 ± 0.04	0.09 ± 0.01	0.07 ± 0.01
	Control	5.15 ± 0.09	-	-	1.17 ± 0.63	0.22 ± 0.09	0.10 ± 0.02
	Ash	5.12 ± 0.10	-	-	1.50 ± 0.90	0.26 ± 0.11	0.11 ± 0.02
	Biochar	5.28 ± 0.14	-	-	1.54 ± 0.67	0.30 ± 0.11	0.17 ± 0.05
	Ash+biochar	5.17 ± 0.07	-	-	1.31 ± 0.57	0.21 ± 0.007	0.11 ± 0.02

There was a large difference in the overall (i.e. all provenances) seedling survival rate between the two sites throughout the experiment (Figure 11a). At the last survey, seedling survival rate was 45

% in site 1 and 74 % in site 2. The difference in survival rate widened between the two sites as early as June 16th and averaged 30.5 % for the remainder of the survey. Seedling survival rate also displayed a similar overall pattern at both sites. Independent of sites, seedlings planted in exclosures (protected) showed a final survival rate of 65.8% while unprotected seedlings showed a survival rate of 53.2% (Figure 11b). The difference between the protected and unprotected seedlings widened on June 20th but it stabilized at the next survey, i.e. June 26th. Thereafter, survival rate between protected and unprotected seedlings followed a similar pattern and the difference between the two averaged 11.9 % for the remainder of the survey. Seedling survival rate largely varied as a function of acorn provenances (Figure 11c).

At the end of the survey, seedling survival rate was highest for the MR provenance (79.2 %), followed by IA (59.7 %), PC (55 %) and SBL ((43.8 %). Survival rate of the MR, PC and SBL provenances widened early in the survey (between June 14th and 16th) and differences were then maintained for the rest of the survey. While seedling survival rates stabilized by July 4th, survival rate of the IA provenance decreased steadily throughout the survey as soon as it was planted. However, we did observe a short respite in mortality between July 24th and August 2nd. Seedling survival rates displayed smaller variation between soil fertilization treatments (Figure 11d). The highest survival rate was observed under the ash + biochar treatment at 61.6 %, followed by the biochar treatment at 63.6 %, the control treatment at 58.8 % and the ash treatment at 54 %. Overall, seedling survival patterns were similar between fertilization treatments, although the ash treatment initially performed strongly, i.e. 84.1 % survival rate between June 16th and 20th, it underperformed relative to the other treatments thereafter. Conversely, the ash + biochar treatment exhibited the lowest survival rate early in the survey, but it was ultimately the treatment with the highest survival rate at the end of the experiment.

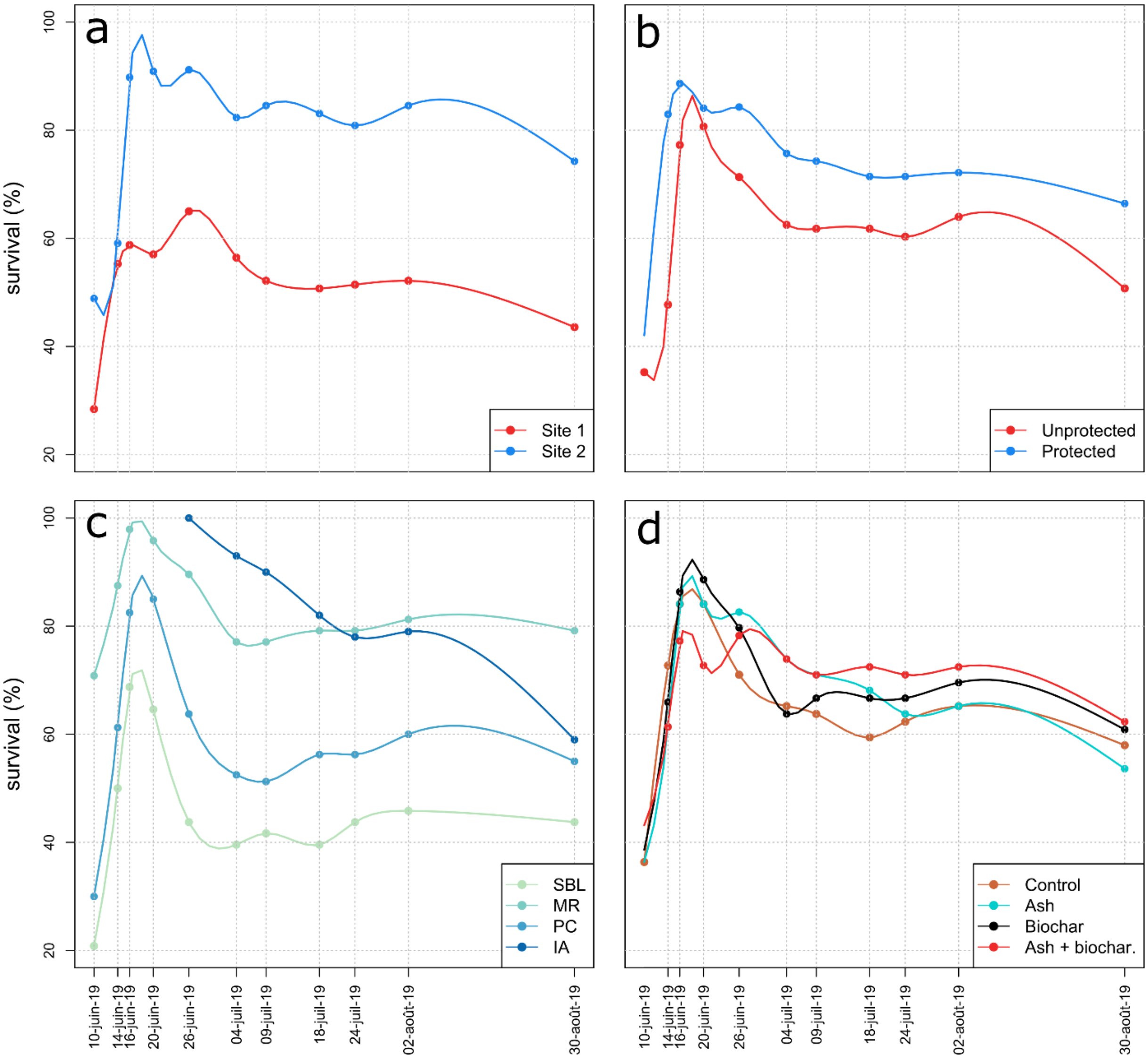

Figure 11. Red oak seedling survival rates in the experimental plots at SBL during the 2019 ssurvey as a funtion of site (a), protection against large herbivory (b), acorn provenance (c) and soil fertilization (d). The initial rise in survival rates is the result of some seedlings showing vitality (i.e. leaf development) several days after transplantation.

Table 9. One-factor ANOVA test results of red oak seedling survival and growth development variables measured as a function of site, protection against large herbivory, acorn provenance and soil fertilization. The IA provenances was tested separately because itis a younger seedling and was planted a couple of weeks after the other three provenances. P<0.05 is considered significant for site, while p<0.01 is considered significant for the three other factors (see methods section for justification). All significant differences are identified with *.

Provenance	**Response variable**	**Factors**		
		Site	**Protection**	**Fertilization**
SBL, MR & PC	Survival rate (%)	1.2e-05*	0.09*	0.30
	Number of leaves	0.045*	0.43	0.31
	Total leaf area (cm²)	0.0015*	0.73	0.17
	Mean area / leaf (cm²)	0.033*	0.018*	0.24
	Final stage reached	0.0015*	0.30	0.26
	Max. stage reached	0.0092*	0.71	0.070*
	Stage regression	0.0243*	0.012	0.30
	Survival time (weeks)	0.00016*	0.86	0.45
	Relative survival time (%)	0.00016*	0.86	0.45
IA	Survival rate (%)	0.16	0.50	0.054*
	Number of leaves	0.060	0.17	0.72
	Total leaf area (cm²)	0.78	0.17	0.54
	Mean area / leaf (cm²)	0.049*	0.33	0.77
	Final stage reached	0.04*	0.085*	0.18
	Max. stage reached	0.38	0.09*	0.51
	Stage regression	0.067	0.55	0.16
	Survival time (weeks)	0.047*	0.41	0.39
	Relative survival time (%)	0.047*	0.41	0.39

The one-factor ANOVA tests show that site had a significant effect on the seedling survival of the SBL, MR and PC provenances as well as all other growth development variables measured (Tables 3.3.2 and 3.3.3). All data indicate that seedlings at site 2 outperformed seedlings at site 1 in regard to survival and growth development. Statistical testing also suggests that protection against large herbivory led to higher seedling survival, mean area per leaf and stage regression (Tables 3.3.2 and 3.3.3). A higher stage regression was observed for protected seedlings, which mean that seedlings exhibit a larger difference between the maximum and final growth stage achieved. Finally, soil fertilization significantly affected the maximum stage achieved by the SBL, MR and PC seedlings, with an average of 2.37 under the control, 3.44 under ash, 2.98 under biochar and 3.81 under ash + biochar.

Figure 12. Pictures captured with the Wingscape cameras. Squirrels (a: Sciurus sp.), flying squirrels (b: Glaucomys sp.) and North American porcupines (c: Erethizon dorsatum) are seen foraging red oak acorns in the experimental plots. White-tailed deer (d: Odocoileus virginianus) also often visited the plots, although we have no picture of them directly foraging acorns or browsing on seedlings.

The IA provenance also performed better at site 2, although the differences between sites were not as obvious as the SBL, MR and PC provenances (Tables 9 and 10). The IA seedlings at site 2 outperformed seedlings at site 1 in regard to mean area per leaf, final growth stage reached and survival time. Seedling survival rate was also marginally significant at $p = 0.1$ (i.e. 14.0 % higher at site 2 than site 1). Seedling protection against large herbivory led to significantly lower maximum and final growth stages reached, which is contrary to SBL, MR and PC seedlings (Tables 9 and 10). The IA provenance showed higher but non-significant survival rates in protected plots than in unprotected ones, while significantly higher maximum and final stages reached highlight the effectiveness of exclosures for IA seedling growth. Many pictures of white-tailed deer were captured at both sites, suggesting potentially significant browsing of red oak seedlings (Figure 12). Soil fertilization only had a significant effect on survival rates (Tables 9 and 10) of IA seedlingsurvival rate under the control, ash, biochar and ash + biochar treatments were respectively 63.6 %, 40.8 %, 78.1 % and 56.4 %

The SBL seedlings exhibited the lowest values for most response variables measured compared to the other provenances (Table 11). Survival rate, number of leaves, final growth stage reached and relative survival time of SBL seedlings were significantly lower than the other provenances. The MR seedlings exhibited greater performance than the SBL and PC provenances in terms of survival, number of leaves, total leaf area, final and maximum stage reached, survival time and relative survival time, but only survival time and relative survival time were significantly higher than the SBL and PC seedlings (Table 11). Finally, the IA seedlings exhibited a relative survival time similar to the MR seedlings, whereas survival rate was 59.7 % and not statistically different from the SBL and PC provenances. An increase in mortality of the IA seedlings occurred near the end of the survey (see Figure 11). Yet, the IA seedlings exhibited significantly greater total leaf area and final and maximum growth stage reached.

Table 10. Mean ± standard errors of seedling survival and growth development variables measured as a function of site, protection against large herbivory and soil fertilization. Letters indicate significant differences for each variable tested with one-factor ANOVA (see Table 9).

Provenance	**Response variable**	**Site**		**Protection**		**Fertilization**			
		1	**2**	**Without**	**With**	**Control**	**Ash**	**Biochar**	**Ash+biochar**
SBL, MR & PC	Survival (%)	40.0 ± 6.66^{a}	78.8 ± 4.27^{b}	51.2 ± 6.79^{a}	67.5 ± 6.58^{b}	55.7 ± 11.5	62.8 ± 7.16	53.9 ± 10.6	65.0 ± 9.71
	Number of leaves	2.59 ± 0.44^{a}	3.59 ± 0.22^{b}	3.29 ± 0.33	2.89 ± 0.39	2.83 ± 0.57	3.63 ± 0.50	2.43 ± 0.42	3.46 ± 0.50
	Total leaf area (cm²)	5.57 ± 0.99^{a}	9.90 ± 0.81^{b}	7.49 ± 0.90	7.98 ± 1.11	6.0 ± 1.35	9.23 ± 1.41	6.3 ± 1.16	9.41 ± 1.57
	Mean area / leaf (cm²)	2.24 ± 0.17^{a}	2.72 ± 0.13^{b}	2.28 ± 0.14^{a}	2.80 ± 0.15^{b}	2.09 ± 0.20	2.61 ± 0.23	2.60 ± 0.16	2.70 ± 0.25
	Final stage reached	2.04 ± 0.32^{a}	3.26 ± 0.16^{b}	2.86 ± 0.27	2.44 ± 0.30	2.09 ± 0.43	2.93 ± 0.33	2.46 ± 0.41	3.12 ± 0.41
	Max. stage reached	2.62 ± 0.35^{a}	3.68 ± 0.18^{b}	3.07 ± 0.26	3.23 ± 0.32	2.37 ± 0.45^{a}	3.44 ± 0.30^{ab}	2.98 ± 0.38^{ab}	3.81 ± 0.42^{b}
	Stage regression	1.03 ± 0.18^{a}	0.66 ± 0.09^{b}	0.63 ± 0.09^{a}	1.04 ± 0.16^{b}	0.82 ± 0.18	0.71 ± 0.16	0.77 ± 0.13	0.97 ± 0.26
	Survival time (weeks)	5.34 ± 0.75^{a}	8.73 ± 0.34^{b}	6.95 ± 0.53	7.12 ± 0.81	6.30 ± 1.22	7.14 ± 0.84	6.43 ± 1.00	8.28 ± 0.69
	Relative survival time (%)	48.5 ± 6.83^{a}	79 ± 3.09^{b}	63.2 ± 4.78	64.7 ± 7.34	57.2 ± 11.1	64.9 ± 7.61	58.4 ± 9.08	75.3 ± 6.27
IA	Survival (%)	52.7 ± 6.34	66.8 ± 7.47	56.3 ± 6.65	63.1 ± 7.54	63.6 ± 7.76^{ab}	40.8 ± 10.7^{a}	78.1 ± 11.5^{b}	56.4 ± 5.51^{ab}
	Number of leaves	4.05 ± 0.30	3.34 ± 0.21	3.96 ± 0.27	3.44 ± 0.26	3.77 ± 0.28	4.02 ± 0.41	3.42 ± 0.18	3.58 ± 0.57
	Total leaf area (cm²)	14.3 ± 1.14	14.8 ± 1.41	15.8 ± 1.18	13.3 ± 1.30	14.2 ± 1.48	16.5 ± 2.11	14.9 ± 1.90	12.7 ± 1.68
	Mean area / leaf (cm²)	3.62 ± 0.22^{a}	4.39 ± 0.30^{b}	4.20 ± 0.37	3.81 ± 0.15	3.86 ± 0.47	4.16 ± 0.43	4.27 ± 0.36	3.73 ± 0.35
	Final stage reached	2.78 ± 0.38^{a}	4.12 ± 0.50^{b}	4.02 ± 0.45^{a}	2.88 ± 0.46^{b}	3.90 ± 0.49	2.56 ± 0.79	4.40 ± 0.82	2.94 ± 0.31
	Max. stage reached	5.41 ± 0.30	5.85 ± 0.39	6.05 ± 0.38^{a}	5.21 ± 0.29^{b}	5.77 ± 0.51	5.67 ± 0.52	6.07 ± 0.47	5.02 ± 0.50
	Stage regression	2.64 ± 0.40	1.73 ± 0.27	2.03 ± 0.25	2.33 ± 0.43	1.87 ± 0.40	3.10 ± 0.66	1.67 ± 0.47	2.08 ± 0.33
	Survival time (weeks)	5.51 ± 0.26^{a}	6.23 ± 0.24^{b}	6.02 ± 0.25	5.71 ± 0.72	5.73 ± 0.41	5.42 ± 0.37	6.27 ± 0.36	6.05 ± 0.31
	Relative survival time (%)	78.6 ± 3.69^{a}	89.0 ± 3.36^{b}	86 ± 3.57	81.6 ± 3.89	81.8 ± 5.83	77.4 ± 5.38	89.6 ± 5.21	86.5 ± 4.45

Table 11. Mean ± standard errors of seedling survival and growth development variables measured as a function of acorn provenance. Letters indicate significant differences for each variable tested with one-factor ANOVA. Note that the IA seedlings were younger and planted a few weeks after the other three provenances and thus, comparison of variables should be done with care, notably survival time and relative survival time.

Response variable	**Accorn provenance**				
	ANOVA p-value	**SBL**	**MR**	**PC**	**IA**
Survival (%)	0.011*	43.8 ± 6.66^{b}	79.2 ± 5.99^{a}	55.0 ± 9.75^{ab}	59.7 ± 4.98^{ab}
Number of leaves	0,058*	2.53 ± 0.44^{a}	3.69 ± 0.37^{ab}	3.05 ± 0.47^{ab}	3.70 ± 0.19^{b}
Total leaf area (cm^2)	4.26e-07*	6.34 ± 1.14^{a}	9.38 ± 1.08^{a}	7.49 ± 1.40^{a}	14.6 ± 0.89^{b}
Mean area / leaf (cm^2)	6.07e-08*	2.59 ± 0.22^{a}	2.58 ± 0.19^{a}	2.38 ± 0.18^{a}	4.01 ± 0.20^{b}
Final stage reached	0.071*	2.22 ± 0.39^{a}	3.10 ± 0.24^{ab}	2.63 ± 0.40^{ab}	3.45 ± 0.33^{b}
Max. stage reached	8.93e-10*	2.91 ± 0.42^{a}	3.56 ± 0.22^{a}	2.98 ± 0.40^{a}	5.63 ± 0.25^{b}
Stage regression	1.23e-05*	0.90 ± 0.16^{a}	0.83 ± 0.16^{a}	0.71 ± 0.16^{a}	2.18 ± 0.25^{b}
Survival time (weeks)	0.00016*	5.67 ± 0.92^{b}	9.10 ± 0.30^{a}	6.34 ± 0.87^{b}	5.87 ± 0.18^{b}
Relative survival time (%)	9.8e-06*	51.5 ± 8.37^{b}	82.8 ± 2.69^{a}	57.6 ± 7.93^{b}	83.8 ± 2.63^{a}

The MRT analyses captured survival and growth development stages of all four provenances simultaneously (Figure 13). The regression tree of survival rate (a) highlights the effects of site and provenance. A first separation was made between sites 1 and 2, with site 2 exhibiting higher survival rate than site 1. A second separation was made at site 1 between the provenance groups of MR–IA and SBL–PC. The MR–IA groups had higher survival rate than the SBL–PC group. The regression tree of relative survival time (b) also displays the effects of site and provenance. However, a first separation was made between the acorn provenance groups of IA–MR and SBL–PC. The IA–MR group exhibited higher relative survival time than the SBL–PC group. A second separation distinguished the two groups into site 1 and site 2. Relative survival time was higher for both groups at site 2. The regression tree of maximum growth stage reached (c) and total leaf area (d) led to a first separation between the IA provenance and the provenance group SBL–MR–PC. The SBL–MR–PC group was then subdivided into site 1 and site 2. The IA provenance exhibited the highest maximum stage reached and total leaf area. For the SBL–MR–PC group, maximum growth stage reached and total leaf area were higher at site 2.

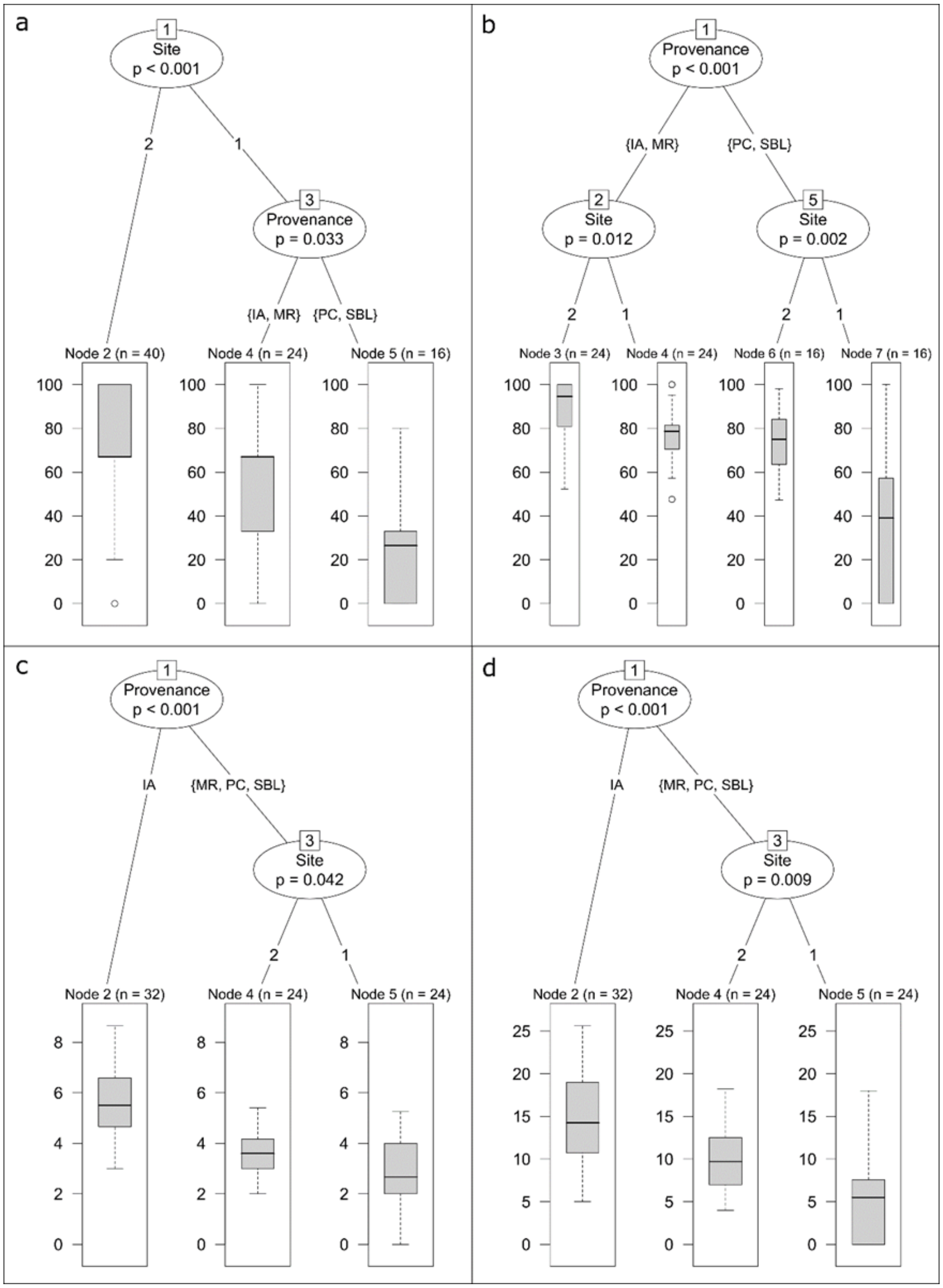

Figure 13. Multiple regression tree of red oak survival rate (a, in %)), relative survival time (b, in %), maximum stage reached (c, classes 1 to 8) and total leaf area (d, in cm2) as function of site and acorn provenance. Other factors tested such as protection against large herbivory, soil fertilization and blocking within site were not significant at p<0.05 and were thus excluded from the analyses.

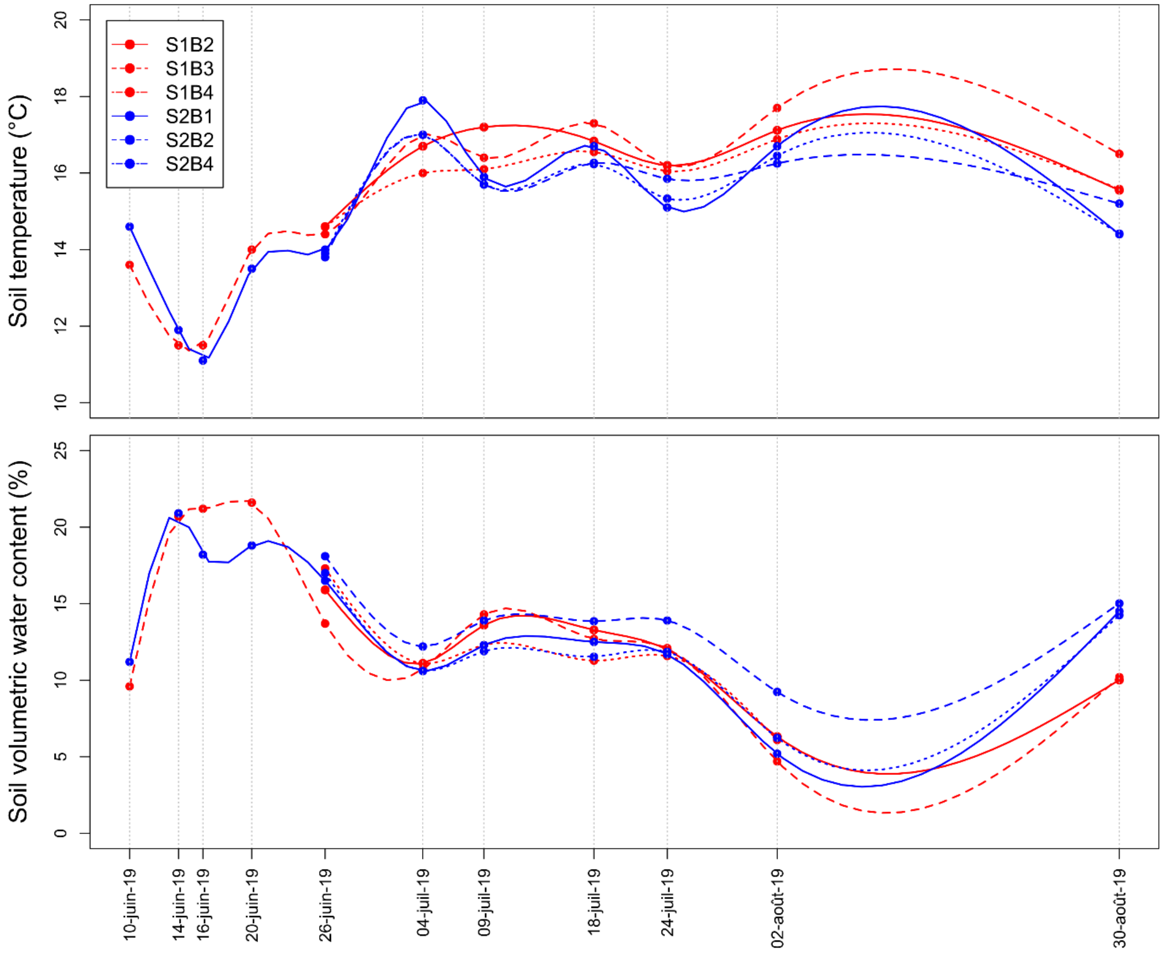

Figure 14. Soil temperature and volumetric water content measured in the experimental blocks at sites 1 (red lines) and 2 (blue lines) during the 2019 survey.

Soil temperatures and volumetric water content were measured throughout the survey at each field sampling period. Figure 14 clearly shows the inverse relationship of the two variables, with the volumetric water content decreasing when temperature is increasing. Soil temperature was minimal at about 11°C on the 16th of June, then started rising and fluctuated between 15°C and 17°C from the 4th of July to the end of august. Volumetric water content contents are highest between the 14th and 26th of June at 15-20%, then maintains itself at around 12-15% in July and hits its lowest value in the beginning of August at 7-8% before rising back to 12-13% at the end of the survey. Site 1 shows slightly higher soil temperatures and lower soil volumetric water content than site 2 throughout most of the summer (from June 26th to 30th of august).

Discussion

The series of studies conducted here have helped portray the main factors responsible for red oak regeneration at SBL. Fire played a significant role in the past but its suppression from the landscape in the last fifty years has led to a series of regeneration failures of the species. Our results suggest that these failures are largely governed by a series of factors such as water availability, light transmission, acorn predation, herbivory and soil nutrients, that act in confounding ways. These factors are schematized by their level of influence on early regeneration in Figure 15 based on statistics and deduction, and are further discussed here. In the absence of fire, our study highlights that site conditions, namely water availability, genetics (provenance) and control of herbivory are key factors to predict germination, survival and growth rates.

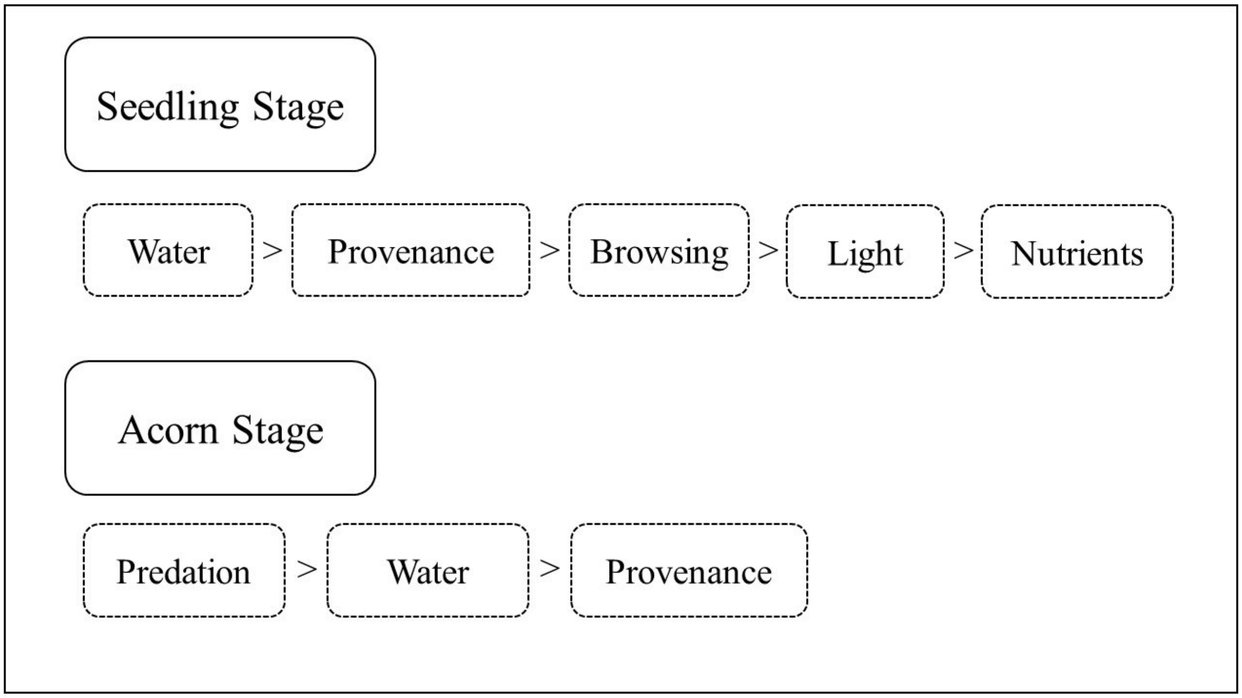

Figure 15. A simplified schematic of factors affecting red oak natural regeneration at acorn and early seedling stages in a decreasing order of importance at SBL.

Stand history

The oldest trees at sites 1 and 2 date back to 1920, which points to a wildfire affecting much of the SBL area (Savage, 2001; Bélanger et al. 2002). While both red oak and sugar maple are the dominant tree species at the sites, the cohort recruitment pattern at each site are different. On the one hand, site 1 shows a greater dominance in red oak, mostly established between 1920 and 1940, with some subsequent regeneration from competing sugar maple. It has greater overall red oak biomass. On the other hand, site 2 exhibits a more concurrent and longer establishment period of red oak and sugar maple trees, the former showing a lower frequency but demonstrating a clear growth advantage from the initial cohort establishment. The red oak trees are, however, smaller in size in comparison to site 1, thus also resulting in lower biomass. Fire disturbance severity, frequency and timing may have played a role in the resulting tree species composition and age structure of these red oak stands (Crow, 1988; Abrams, 1992; Signell et al., 2005). Brose (2010) suggested that red oak regeneration is dominant after a medium or high intensity burn applied during either spring or summer, while red maple and yellow poplar regeneration dominate plots after low intensity burns, regardless of timing. In this regard, observed differences in stand tree species composition and density between sites 1 and 2 is likely the result of a divergence in fire severity. This is also in alignment with the fact that the regenerative strategy of red oak is mainly derived from its sprouting ability (Sander, 1990) rather than a physical resistance to fire (in comparison to other oak and hardwood species), with higher fire severity advantaging red oak regeneration because it eliminates mature trees of competing species. Fire disturbance characteristics such as fire temperature and fuel load can also influence the overall quantity of charcoal produced, which is positively correlated with base cation availability at SBL and can alter soil chemistry and nutrient availability over decades (Bélanger et al., 2004).

Water and light availability

Site was found to be the most significant factor controlling planted red oak seedlings survival and growth differences in the field experiment. Seedlings at site 2 performed better than site 1 for all response variables tested. In this respect, stand characteristics may well provide insights as to the main drivers of red oak regeneration at the sites. Moreover, tree density, species composition and basal area differed more largely between the sites than soils, thus indicating that stand characteristics are more largely influencing red oak regeneration. Site 2, where seedling survival and growth rates were higher, exhibits much greater tree species diversity and density but lower basal area. Fei et al. (2003) found a strong relationship between cover species and density of red oak regeneration, with a steep decrease under any other species than itself. However, this is contradictory to our results. Rather, we argue that the diversified canopy cover at site 2 was beneficial to red oak seedling survival and growth during periods of low water availability.

Although red oak saplings and mature trees are resistant to water stress, seedlings are yet vulnerable to such pressures, especially prior to extensive root system development (Kolb et al., 1990; Bauweraerts et al., 2013). For the most part of the 2019 summer, soils at site 1 were warmer and dryer than soils at site 2. We argue that the colder and wetter soil conditions at site 2 were due in part by a larger presence of American beech, mostly saplings which were unaccounted for in the basal area measurements. American beech is associated with lower light transmission in the SBL stands (Collin et al. 2017, 2018). As a result, beech can also limit overheating of understory vegetation and soils and reduce water losses from evapotranspiration. Overall, soils in stands containing some beech at SBL have generally lower temperature and higher moisture (Bélanger et al. 2021). In theory, the less biomass at site 2 should also be associated with lower losses from evapotranspiration. This difference in soil water availability may explain the divergence in survival and growth rates of red oak seedlings between the sites. During field measurements, symptoms of water stress such as dried leaves were often observed on experimental seedlings before their death, notably at site 1, which concurs with the explanation of red oak seedling mortality due to water constraints. Kleiner and al. (1992) have also proposed that red oak seedling shoot growth can be significantly (negatively) impacted by water stress. The 2019 summer at SBL was slightly warmer and dryer than normal, suggesting that water stress was a significant factor affecting survival and growth that specific year. In this respect, germination and seedling establishment will likely be a critical phase under climate change, but as red oak seedlings develop their root system, they should become less vulnerable to water stress (Crow, 1988; Sander, 1990). Thus, this could also mean that planting larger caliber seedlings with larger roots will be key for assisted migration of red oak.

Measurements of LAI suggest more leaf surface area in site 2. We suspect tree species composition, notably higher American beech regeneration, is responsible for this difference. Messier and Bellefleur (1988) have shown that spectral irradiance of the forest floor (W/m^2) is lower under American beech than under sugar maple and yellow birch at climax stage. Similar results were reported by Collin et al. (2018) at SBL. Furthermore, Canham and Burbank (1994) found that light is at < 2 % of full sun under American beech canopy, while it is at > 5 % under red oak canopy. Our results at site 2 thus suggest that lower light availability does not negatively impact the performance of red oak seedlings. Conversely, Phares (1971) observed that while red oak seedlings accumulate nutrients under heavy shade (e.g. 10 % of light availability), height growth is triggered only at a light availability threshold of 30 % light or more, and the highest biomass increments were measured at full sunlight. This implies that higher light availability at site 1 is most likely not responsible for poor seedling performance and corroborates the idea that soil water availability played a more significant role in early seedling survival and growth.

Provenance and genetic adaptation

Provenance had a significant impact on germination and growth in the greenhouse as well as seedling survival and growth in the field. The results in both experiments highlight the importance of provenance quality in the red oak regeneration process, and the relationship between site conditioning, genetic adaptations and seedling growth and survival. This is especially important to highlight as acorn and seedling stock quality are significant factors to consider for red oak seedling development (Buchschacher et al., 1991; Ward et al., 2000; Lombardo and McCarthy, 2009).

Contrary to the MR and PC provenances, the SBL provenance underperformed under the higher soil richness level in the greenhouse. Interestingly, the SBL provenance also underperformed in the field experiment compared to the other provenances, whether fertilized or not. The literature supporting seed source effects on red oak early regeneration is scarce, but there are a few cases that help validate our inferences. For example, McGee (1974) found that seed source elevation can affect seedling budbreak, bud and leaf development and height. Furthermore, Abrams (1994) found that adjacent red oak stands can exhibit distinct genotypes as a result of contrasting microenvironments. Notably, they observed that differences in water availability and drought effects within a limited geographical range created differences in net photosynthetic rates and leaf water potential within the red oak provenances studied.

Two explanations are thus proposed for the poor performance of the SBL provenance. First, of the acorns collected for the germination and seedling studies, acorn infection rates by *curculio* weevils were highest for the SBL provenance (77 %), whereas the MR and PC provenances had much lower infection rates at 25 % and 22 % respectively. Fierke et al. (2007) showed that red oak borer (*Enaphalodes rufulus*) population density was respectively positively and negatively correlated with the number of red oak tree and tree species diversity. Higher distance between individual trees and higher tree species diversity may thus act as barriers for parasitic insects and enhance acorn survival. Furthermore, damage to the cotyledon was shown to negatively impact red oak acorn germination rate and seedling performance (Yi et al., 2019) because germination and early growth of red oak seedlings are highly dependent on acorn nutrient reserves (Yi et Wang, 2015). Damaged acorns were identified and discarded as best as possible in our study. Yet, it is possible that a lower performance of the SBL provenance seedlings in our experiments could be due to a higher proportion of poor quality SBL acorns in our final batch. Second, the poor performance of SBL acorns in the greenhouse could indicate that this provenance was genetically selected to perform better under more acidic and nutrient-poor soil conditions. Specifically, we suspect that the SBL provenance performed poorly under the highest soil richness in the greenhouse because of the forms of N available under that specific treatment. The ratio of NO_3-N/NH_4-N as measured by PRS probes was 0.73, 0.80 and 2.72 under the low, medium and high soil richness levels, respectively. In comparison, Bélanger et al. (2004) found NO_3-N/NH_4-N ratios in surface soil solutions to vary between 0.29 and 1.39 in various stands at SBL. We thus suggest that the high soil richness treatment provided plenty of N for plant growth but not in the correct form for optimal germination and growth of the SBL provenance. For other provenances, we do not have soil data, but we believe they tend to grow under more neutral soil conditions which produce NO_3-N rich environments. Our speculation is based on the MR soils being formed from mafic rocks, notably gabbro, the PC soils being formed mostly from felsic rocks such as granitoïd gneiss but marble outcrops are also abundant in the area and were mixed in the glacial till, and the IA soils being formed from limestone and dolomite.

In addition, seedlings from the MR provenance, which is the southernmost provenance, exhibited the highest survival rate in the field experiment by as much as 33 % in comparison to the other provenances. The MR site is also less elevated than the SBL site (230 m vs. 375 m). Again, acorn quality may explain, in part, the more vigorous seedlings. These acorns were, as a whole, larger and showed a lower infection rate by weevil. The superior field performance of the MR provenance might also result from the meteorological conditions that prevailed during the 2019 growing seasons. This growing season was warmer and dryer than normal, especially in the spring (May to June) (MELCC, 2021a). These conditions may have been conducive to the more southern MR provenance than the other provenances. For example, it is possible that the MR provenance was able to deal better with water stress despite limited root development, whereas the SBL provenance could have been more susceptible to dry spells. The MR provenance may have also performed better because southern provenances are expected to grow sooner in the spring, and this timing would have corresponded to more suitable growing conditions at SBL (e.g. cooler and wetter). The result in respect to the MR provenance is in support with the general idea that there will be a northern shift in the distribution of red oak in northeastern North America and that climate change should be beneficial to its expansion (Zolkos et al., 2015; Iverson et al., 2019; Prasad et al., 2020). Our work thus suggests that conducting this type of research over several planting years may better highlight how provenances from different climate envelops will cope with the future climate. It may also help find the proper provenances for assisted migration (McLachlan et al., 2007; Pedlar et al, 2012; Williams et Dumroese, 2013) based on climate analogues (Dessai et al., 2004; Salinger et al., 2005) and not just based on investigation of provenances *per se*. For example, the MR provenance has done particularly well when it was planted during a warm/dry summer, but a very different (negative) outcome could have been observed if it had been planted during a cold/wet summer.

Acorn predation and large herbivory

Acorn predation and leaf herbivory had significant impacts on red oak regeneration. The most severe impact was with acorn predation. We associate the failed germination study in 2018 mostly to high predation. Regardless of provenance, acorns were almost entirely consumed by local fauna, mainly chipmunks (*Tamias striatus*), when planted in May 2018. The 2018 summer was also one of the warmest in record (MELCC, 2021b), and this has likely participated in the dessication of acrons. Second, browsing impacted seedling survival for SBL, MR and PC provenances, but only affected overall growth marginally. Blossey et al. (2019) showed a substantial difference in red oak seedling growth rate induced by browsing, whereas Buckley et al. (1998) found that the removal of plant competitors can enhance the pressure from deer browsing on red oak seedlings. Thus, this factor can be of significant importance for red oak regeneration, and its apparent effect on growth may increase after several growing seasons.

Soil nutrients

In turn, water limitations in 2019 likely overshadowed the effect of soil nutrient supply and fertilization on red oak seedlings. Soils are often identified as a main descriptor of site quality and suitability for given species (Mason, 1946; Nowacki et al., 1990; Nowacki et Abrams, 1992; Rajakaruna, 2017; Hulshof et al., 2020). This also implies that soil conditions play a substantial role in regard to red oak seedling regeneration dynamics. The literature regarding red oak describes the species as striving on nutrient poor, acidic, uphill mesic sites (Crow, 1988; Sander, 1990), a description that suits both our study sites. As a whole, sites 1 and 2 exhibited similar acid-base status in the forest floor, but the mineral soil at site 1 showed higher exchangeable base cation concentrations. This difference in soil quality could also partially explain the difference in red oak seedling survival and growth observed between the sites. Lower mineral soil quality at site 2 is linked to overall greater seedling performance. This corroborates previous findings that red oak performs particularly well under soils of low fertility (Frank et al., 2018). Such sites apparently favor red oak trees because of the limiting conditions restraining competitor species, well-drained soils and disturbance regimes. Red oak is also reported to grow on a wide variety of sites (Tirmenstein, 1991), but there are too many confounding factors (e.g. water and light availability, stand structure and diversity, etc.) at play to pinpoint the mineral soil as a significant influence of red oak regeneration in this study.

There is no doubt that tree diversity and canopy cover differences between sites 1 and 2, whether they are a result of past fire disturbance or not, can have a large effect on soil chemical properties by affecting biocycling. However, most of the effects of species composition on soil properties are mainly observed in the forest floor where the influence of litter decomposition and nutrient are large (Berg, 2000; Bélanger et al., 2004). For example, Finzi et al. (1998) found that interspecific differences in soil properties under different tree species composition, including red oak stands. They found that pH and total C were higher and net N mineralization was lower under red oak stands than sugar maple and American beech stands, thus suggesting generally low quality and decomposability of red oak litter. Forest floor pH at the more diversified site 2 exhibited slightly higher values than site 1, but overall, it does not seem probable that tree species diversity and density variation led to soil conditions that were more favorable to red oak seedling survival and growth at one site (site 2) over the other (site 1). The fact that ash and biochar fertilization have, for the most part, not shown a significant increase in seedling survival and growth at either site reinforces the idea that soils with higher pH and nutrient availability, as seen for the forest floor at both sites following ash and biochar application, are not more conducive to red oak.

Conversely, the results from the greenhouse experiment suggest that a significant and positive effect of soil nutrient availability is expected on germination, growth and survival of red oak seedlings. The greenhouse experiment was conducted under ideal growing conditions in regard to light and water availability as well as air temperature. There was also no issue with insect herbivory and disease during the experiment. As such, the diverging results between the field and greenhouse experiments imply that the absence of an effect of soil nutrients on red oak planted in the field was due to the presence of more significant and confounding limiting factors. This is also highlighted by the success of red oak establishment in Europe in the absence of fire disturbance as well as situations where the species is considered invasive (Riepšas and Straigytė, 2008; Langmaier and Lapin, 2020). Explanations for this include lower predation from local fauna and higher shade tolerance than indigenous oak species (Major et al., 2013; Nicolescu et al., 2020). In our study, unstressed red oak seedlings (greenhouse)took full advantage of increased nutrient availability for growth, whereas stressed seedlings (field) did not use nutrients with the same efficiency to survive and produce biomass (Kolb et al., 1990; Kleiner et al., 1992). Our results thus suggest that other factors, such as water and perhaps light or predation, are playing a larger role than soil nutrients in governing red oak establishment and growth at SBL.

It should be considered, however, that the absence of a response of red oak seedlings to ash and biochar fertilization could be due to a delay for nutrients to be absorbed by the roots. Indeed, several studies show a delayed response of plants to ash fertilization (Reid and Watmough, 2014, Bélanger et al. 2021). Root length and radius, or more specifically total root surface area, influence plant nutrient uptake (Barber and Silberbush, 1984). As such, the small root system of the planted seedlings likely had a low capacity for sequestering the nutrients added from the ash. This could also stem from the fact that while the benefits of ash fertilization on the forest floor occurs quickly, the response of the mineral soil is slower as it takes more time for the nutrients to migrate further down and react with soil exchangeable surfaces (Reid and Watmough, 2014, Brais et al., 2015). Despite that we fertilized in the fall, 6 months prior to planting the following spring, and re-fertilized the following fall, there is always a possibility that the benefits of fertilization on foliar nutrition and growth of red oak seedlings could increase with time. Kolb and al. (1990) have shown that, at higher soil fertility and in the absence of light or water stress, yellow poplar performs better than red oak. Thus, since red oak is outpaced by late-successional or more shade-tolerant competing species, regeneration of the species may not benefit much from higher soil nutrient availability in the presence of limitations of other resources. The von Liebig's law of the minimum specifies that plant growth is modulated by the scarcest resource, e.g. a specific nutrient limiting plant growth among a series of plant nutrients (van der Ploeg et al., 1999). The concept applies well to individual trees, although it may not apply so well to the ecosystem scale as new plant trajectories (e.g. new species) are bound to emerge when a resource becomes limiting (Danger et al., 2008).

Conclusion

In this study of red oak at the northern limit of its distribution, we observed that the species remained dominant in the two studied stands throughout the 20th century but is now showing regeneration failure. Furthermore, stands are shifting towards more shade-tolerant, late successional species such as American beech, but more research is needed to ecological succession and regeneration dynamics. Our data also suggest that fire played a role in the establishment of red oak and succession of sugar maple and this is corroborated by previous research, with red oak stand age structure dating to the last known fire disturbance occurrence. Although red oak trees were dominant in both stands, variability in tree species composition and density between stands suggests that regeneration dynamics differed substantially. This result may be due to differences in pre-fire species composition, fire frequency/severity and site physical characteristics such as slope direction and aspect. Our study also displayed the importance of other factors in the regeneration process of red oak trees at this latitude. Site was found to have a significant impact on germination, survival and growth of seedlings. The site with higher LAI showed greater water availability and greater regeneration success. Acorn provenance was also another important factor affecting red oak regeneration. Our work therefore display the need to better characterize the response of red oak to site quality while considering the genetic signatures for optimizing success at early regeneration stages. Furthermore, parasites such as weevils and borers and foraging by small mammals, mostly rodents, were found to have large effects on regeneration at the acorn stage, while deer browsing was found to significantly affect survival, and growth to some extent, at the seedling stage. Finally, soil nutrient availability affected germination, survival and growth positively only when other factors (e.g. water and light) were not limiting. As a whole, our study highlights the need to select sites with adequate water availability, use provenances with proper future climate analogues, and protect seedlings against herbivory to maximize regeneration success. Fertilization with wood ash will likely only be beneficial if other conditions are met.

Conclusion générale

Cette recherche montre que plusieurs facteurs affectent la régénération du chêne rouge à la limite nordique de son aire de répartition. L'analyse de la structure et de la composition en espèces des chênaies à la SBL ainsi que la dendrochronologie effectuée sur les carottes d'arbres prélevées montrent que le chêne rouge était l'espèce dominante sur les deux sites pendant le 20ème siècle. Toutefois, depuis quelques décennies, le chêne rouge ne parvient plus à s'y régénérer et on y observe désormais une transition vers des espèces de succession tardive plus tolérantes à l'ombre tel que le hêtre à grande feuille. Les données suggèrent également que le feu a pu jouer un rôle dans l'établissement du chêne rouge et de l'érable à sucre sous son couvert, ce qui concorde avec les études antérieures. Bien que les chênes rouges soient l'espèce dominante dans les deux sites, la variabilité de la composition des espèces et la densité des arbres indiquent que la dynamique de régénération des deux sites diffère de manière importante. Ceci est possiblement dû à des différences au niveaux des d'espèces présentes avant les perturbations par le feu, de la sévérité ou de la fréquence de ces perturbations et des caractéristiques physiques des sites, telles que l'angle ou l'orientation de la pente.

Cette recherche illustre également l'importance de plusieurs facteurs dans le processus de régénération du chêne rouge à cette latitude. Le site a eu un impact significatif sur la germination, la survie et la croissance des semis. Le site présentant un indice de surface foliaire (LAI) plus élevé était caractérisé par une plus grande teneur en eau dans le sol et une plus grande survie des semis de chêne rouge. Les résultats obtenus montrent également que la provenance des glands a eu un impact significatif sur la régénération du chêne rouge. Cette étude met en évidence la nécessité de mieux caractériser la réponse du chêne rouge en fonction de la qualité des sites, tout en considérant les signatures génétiques et les adaptations pour maximiser les chances de succès aux stades juvénile de régénération du chêne rouge. L'attaque des glands par des parasites comme le charançon du chêne ou les petits mammifères, principalement des rongeurs, ainsi que la dessiccation des glands à cause des fortes chaleurs de l'été 2018, une année record pour le Québec, ont eu un effet important au stade de gland, réduisant drastiquement la survie. Au stade de semis, le broutage par le cerf a eu un effet significatif sur la survie et sur la croissance dans une moindre mesure. Enfin, le degré de fertilité du sol n'a eu un effet sur la germination, la survie et la croissance que lorsque d'autres facteurs (par ex. l'eau et la lumière) n'étaient pas limitants. Dans son ensemble, cette recherche souligne l'importance de sélectionner des sites avec une disponibilité en eau adéquate (bien drainés, mais non xériques), d'utiliser des provenances avec les analogues climatiques futurs appropriés et de protéger les plants contre l'herbivorie afin the maximiser le succès de la régénération du chêne rouge. La fertilisation avec de la cendre de bois ou le biochar peut être considérée, mais cette option sera vraisemblablement positive seulement si les autres facteurs ne sont pas limitants.

Étant donné la valeur potentielle du chêne rouge aux niveaux commercial et écologique, ces applications devraient être considérées dans la planification et l'aménagement des futures forêts québécoises puisque l'on s'attend à un décalage de la limite nordique de l'aire de répartition du chêne rouge vers de plus hautes latitudes sous les effets des changements climatiques. Malgré cette extension nordique théorique, plusieurs aspects de la migration potentielle du chêne rouge sous les changements climatiques demeurent incertains, notamment sa vitesse de migration (dispersion des glands) et les changements aux conditions hydriques lors de la saison de croissance. Bien que le chêne rouge est une espèce bien adaptée aux conditions de sécheresse et que les projections mathématiques suggèrent un futur relativement intéressant pour l'espèce, il y a un réel souci de la performance de l'espèce aux stades juvéniles de développement. Est-ce le chêne rouge pourra se régénérer naturellement ? Si oui, à quel niveau d'efficacité et à quelle vitesse ? Faut-il compter sur la migration assistée pour maintenir l'espèce dans le paysage québécois ? Ainsi, il faut souligner ici la nécessité de poursuivre les travaux de recherche afin de mieux comprendre la régénération naturelle du chêne rouge et de proposer des solutions d'adaptation face au climat changeant.

Plusieurs pistes de recherches futures sur la régénération du chêne rouge semblent donc propices, dont l'étude exhaustive de la relation entre les provenances et les conditions de site ainsi que l'exploration du potentiel de régénération du chêne rouge au-delà de son aire de répartition dans une optique de migration assistée. Pour un projet de doctorat, par exemple, un dispositif qui incorporerait un gradient latitudinal de sites receveurs et caractérisés par différentes qualités de station (ex. drainage, aspect, nutriments) et qui viserait plutôt à tester la survie et la croissance de semis de chêne rouge de différents calibres et de diverses provenances permettrait sans doute de développer une stratégie robuste pour sa migration assistée. Dans un tel dispositif, il pourrait également s'avérer intéressant d'étudier l'établissement du chêne rouge dans une ou des aires récemment perturbées par le feu à sa limite nordique afin de tester sa régénération dans des conditions post-feu induites naturellement et/ou artificiellement. De plus, puisque le chêne rouge est sensible au manque d'eau au stade juvénile, une expérience pourrait être menée dans l'optique de caractériser la performance (survie et croissance) de plusieurs provenances en fonction d'un gradient de disponibilité en eau, et ce pour des semis correspondant à différents stades de développement (ex. 1 à 5 ans). En combinaison avec un dispositif permettant de réchauffer le sol de certaines parcelles, une telle étude permettrait de déterminer précisément le ou les seuils à partir desquels le chêne rouge sera potentiellement avantagé ou désavantagé par les effets du réchauffement climatique. Ce dispositif pourrait également incorporer les espèces compétitrices principales du chêne rouge afin de mieux mesurer à quel degré ces changements seraient à son avantage. En fin de compte, l'accumulation de ces connaissances devrait permettre de mieux modéliser et identifier les zones propices au chêne rouge au cours du 21$^{\text{ème}}$ siècle et ainsi d'optimiser les chances de succès de sa régénération.

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