# PROTOCOLES DES DIFFERENTES METHODES D’EXTRACTION TESTEES POUR LE DOSAGE DES NSC ISSUS DE LA DYNAMIQUE RAMEALE

# Méthode n°1 : Extraction au mélange ternaire (MeOH, $CH_3OH$, $H_2O$) des sucres solubles

1) Séchage de la poudre :

Sécher les poudres lyophilisées en étuve à 40-50°C (une matinée ou une nuit).

2) Pesée :

Peser 10 mg(*) de matière sèche lyophilisée dans un tube T1.

(*) : *On peut peser de 3 et 6 mg si vraiment peu de matière.*

3) Extraction 1 :

*Passage des composés polaires et apolaires en solution et séparation par rapport aux débris cellulaires.*

- Extraire avec 0,8 ml de **méthanol/chloroforme/eau** (12/5/3, v/v/v).

- Attendre 30 min à 20 °C.

- Centrifuger 10 min à 5°C et 2000 g.

- Récupérer le surnageant dans un tube T2.

- Renouveler l'opération 1 x afin d'épuiser l'échantillon, en joignant le 2ème surnageant au premier.

- Sur le culot résiduel, mettre 1 ml de **méthanol à 60 %** (v/v) et placer au frigo en attente de l'extraction de l'amidon.

4) Extraction 2 :

*Extraction des métabolites polaires (acides organiques, acides aminés solubles, protéines, sucres solubles ...) contenus dans le mélange des 2 surnageants précédents.*

- Ajouter aux surnageants (env. 2,4 ml) :

  2 ml de **méthanol/chloroforme** (v/v).

  0,8 ml d'**eau** distillée.

- Agiter au vortex.

- Centrifuger 5 min à 2000g

- Récupérer la fraction légère incolore (aqueuse) dans un tube T3.

(Attention ! Ne prélever que la phase supérieure).

- Sur la fraction lourde, ajouter 1 ml de **méthanol à 60 %.**

- Agiter au vortex.

- Centrifuger 5 min à 2000g.

- Récupérer la fraction légère et la joindre à la première.

5) Evaporation :

*Conseil : Placer 30 minutes les tubes T3 au congélateur avant de les mettre dans l'évaporateur sous vide pour éviter les rejets lors du pompage.*

*Pendant ce temps mettre en route l'évaporateur sous vide.*

Evaporer à sec dans un évaporateur sous vide (une nuit).

6) Matériel nécessaire :

- -Blouse de labo
- Travail sous hotte ou sorbonne
- Gants jetables imperméables aux solvants
- Spatule de pesée
- Minuteur
- Tubes type eppendorf 2ml à vis
- Tubes polypropylène 5 ml (ou tubes hémolyse en verre renforcé de 6 ml)
- Vortex
- Pipettes 1ml (et embout pipette) et 5 ml
- Ultra-centrifugeuse réfrigérée
- Balance de précision
- Congélateur -20°C
- Evaporateur sous vide
- Glace pilée
- Eau distillée ou ultrapure
- Méthanol
- Chloroforme

**Remarques importantes**:

***** Tubes :

Matières résistant au $CHCl_3$ et $CH_3OH$: verre, polypropylène, polyéthylène (LPDE, HPDE), ou téflon (PFA, PTFE).

Diamètre 13 mm, 6 ml minimum, bouchons (silicone...).

***** Dès que les sucres se trouvent en milieu aqueux (extraction 2), il faut aller vite et éventuellement stocker au froid (-20°C) car ils peuvent subir des transformations ou stocker les tubes à -20°C en attente du dosage.

# Méthode n°2 : Extraction au méthanol 70% à froid des sucres solubles

1) Séchage de la poudre :

Sécher les poudres lyophilisées en étuve à 40-50°C (une matinée ou une nuit).

2) Pesée :

Peser entre 5 et 10 mg de poudre lyophilisée dans un tube **T1** (eppendorf 2ml à vis).

*La fiabilité des dosages dépend intégralement de la finesse de la poudre. Précision de la pesée au 10 ème de mg (donc peser sur une balance suffisamment précise).*

3) Extraction :

- Ajouter 650 µl de méthanol à 70% (méthanol/eau, 7/3, v/v).

- Vortexer.

- Laisser incuber pendant 10 min à température ambiante.

- Centrifuger à 17 000 g pendant 5 min.

- Transférer le surnageant à la pipette dans un tube (T2) de 5mL en polypropylène.

- Répéter l'extraction 2 fois.

- Rassembler les 3 surnageants dans le tube T2.

- Sécher les surnageants dans un évaporateur à rotation sous vide d'air pendant 12 heures.

- Placer le tube T1 contenant le culot insoluble au congélateur à -20°C en attente de l'extraction d'amidon.

4) <u>Evaporation</u> :

*Conseil : Placer 30 minutes les tubes T2 au congélateur avant de les mettre dans l'évaporateur sous vide pour éviter les rejets lors du pompage.*

Evaporer les tubes T2 à sec dans un évaporateur sous vide (une nuit).

Stocker les tubes T1 et T2 bouchés au congélateur à -20°C en attente de l'extraction de l'amidon et du dosage des sucres.

5) <u>Matériel nécessaire</u> :

- -Blouse de labo
- Travail sous hotte ou sorbonne
- Gants jetables imperméables aux solvants
- Spatule de pesée
- Minuteur
- Tubes type eppendorf 2ml à vis
- Tubes de 5 ml polypropylène ou (tube hémolyse en verre 6m ml)
- Vortex
- Pipette 1ml (et embout pipette)
- Ultra-centrifugeuse réfrigérée
- Balance de précision
- Congélateur -20°C
- Evaporateur sous vide (avec piège à froid à -100°C)
- Eau distillée ou ultrapure
- Méthanol

## Méthode n°3 : Extraction à l'éthanol à 80% à chaud des sucres solubles

<u>Séchage de la poudre :</u>

Sécher les poudres lyophilisées en étuve à 40-50°C (une matinée ou une nuit).

1) <u>Pesée</u> :

Peser entre 5 et 10 mg de poudre lyophilisée dans un tube **T1** (eppendorf 2ml à vis).

*La fiabilité des dosages dépend intégralement de la finesse de la poudre. Précision de la pesée au 10 ème de mg (donc peser sur une balance suffisamment précise).*

2) <u>Extraction</u> :

Cette méthode permet d'extraire tous les composés solubles dans l'éthanol et l'eau : les métabolites polaires (acides organiques, acides aminés, sucres…) et des composés apolaires (pigments hydrosolubles …).

*NB : Les sucres peuvent subir des transformations en milieu aqueux (présence d'enzymes), il faut donc les mettre dans un bac de glace pendant les manipulations et les stocker au froid à -20°C*

- Ajouter 1 ml d'éthanol à 80%.
- Vortexer.
- Incuber au bain marie à 80°C pendant 30 mn.
- Centrifuger 10 mn à 10000 g.
- Récupérer grossièrement le surnageant à la pipette dans un tube **T2** (polypropylène, 5 ml ou tube à hémolyse verre 6 ml), maintenir dans la glace.
- Renouveler l'extraction d'extraction 2 fois.
- Evaporation des tubes **T2** (contenant les 3 surnageants soit env. 3 ml) à sec et à froid dans un évaporateur sous vide pendant 5h environ.

3) <u>Evaporation</u> :

*Conseil : Placer 30 minutes les tubes T2 au congélateur avant de les mettre dans l'évaporateur sous vide pour éviter les rejets lors du pompage.*

Evaporer les tubes T2 à sec dans un évaporateur sous vide (une nuit).

Stocker les tubes T1 et T2 bouchés au congélateur à -20°C en attente de l'extraction de l'amidon et du dosage des sucres.

4) <u>Matériel nécessaire</u> :

- -Blouse de labo
- Gants jetables imperméables aux solvants
- Tubes type eppendorf 2ml à vis
- Spatule de pesée
- Minuteur
- Tubes polypropylène 5ml (ou tubes hémolyse en verre 6 ml)
- Bain marie
- Vortex
- Pipette 1ml (et embout pipette)
- Ultra-centrifugeuse réfrigérée
- Balance de précision
- Congélateur -20°C
- Evaporateur sous vide
- Glace pilée
- Eau distillée ou ultrapure
- Ethanol

**ANNEXE N°2**

PROTOCOLES DU DOSAGE DE L'AMIDON POUR LE DOSAGE DES NSC ISSUS DE LA DYNAMIQUE RAMEALE

# Extraction et dosage enzymatique de l'amidon

1) Solubilisation

- Centrifuger les tubes épuisés en sucres solubles, et contenant le culot insoluble 2000G 10 mn.

- Assécher le culot sous vide 15 mn pour éliminer l'alcool.

- Faire une pesée P1 (tube + culot).

- Ajouter 0,9 ml de soude 0,02 N et mélanger au vortex.

- Faire bouillir ½ heure tubes bouchés.

- Refroidir les tubes.

2) Hydrolyse enzymatique

- Ajouter 0,1 ml d'amyloglucosidase (le pH remonte vers 4,6).

- Laisser au bain marie ½ heure à 50°C (tubes bouchés).

- Faire une pesée P2 (tube +culot +extrait glucose).

- P2 - P1 = volume de l'échantillon (volume = poids car densité voisine de 1 : on a de l'eau + 1 peu de glucose).

3) Dosage :

*NB : A effectuer dans la foulée et au froid dans la glace.*

- Centrifuger 10 min à 2000g et 5°C.

- Garder les tubes au froid (glace pilée pendant le dosage).

- Pipetages en µl (microcuve PMMA UV/VIS de 1,6 ml, spectrophotomètre à bande passante < 2 nm).

Volume final : 0,9 ml par micro-cuve.

Mesures de DO à 340 nm.

| | Témoin | Extrait |
|---|---|---|
| **Triéthanolamine** | 250 | 250 |
| **$H_20$** | 540 | 490 |
| **NADP** | 50 | 50 |
| **ATP** | 50 | 50 |
| | | |
| Echantillon | | 50 |
| | Homogénéiser. Lire DO1. Attendre 10 min. | Homogénéiser. Lire DO1. Attendre 10 min. |
| **HK/G6PDH** | 10 | 10 |
| | Homogénéiser. Attendre 15 min. Lire DO2. | Homogénéiser. Attendre 15 min. Lire DO2. |

Volume total 0,9 ml.

Solutions standard : Glucose, 1 $H_2O$ 1,1%. Pour 50 µl DO = 0,39

Calcul de la concentration en g/l : 0,515 x (DO2 – DO1) pour 50 µl d'échantillon.

P<u>rincipe </u>:

Mesure indirecte de la quantité de glucose, basée sur la relation stœchiométrique entre la quantité de glucose de l'extrait et le NADPH formé lors de la réaction enzymatique :

Glucose + ATP ---HK--- > Glucose6P + ADP

Glucose6P + NADP+ ---G6PDH--- > Gluconate6P + NADPH,H+

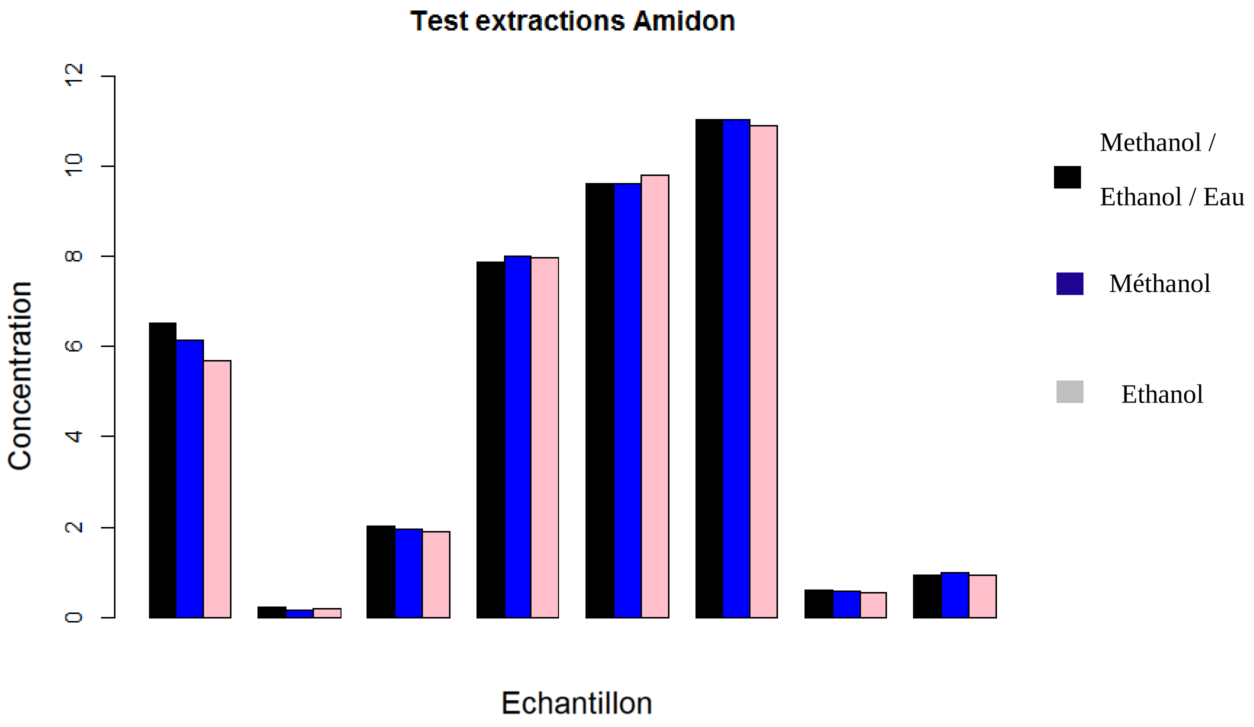
<u>Remarque :</u>

PM (Glucose ou Fructose) = 180,16 g/mole ($C_6H_{12}O_6$)

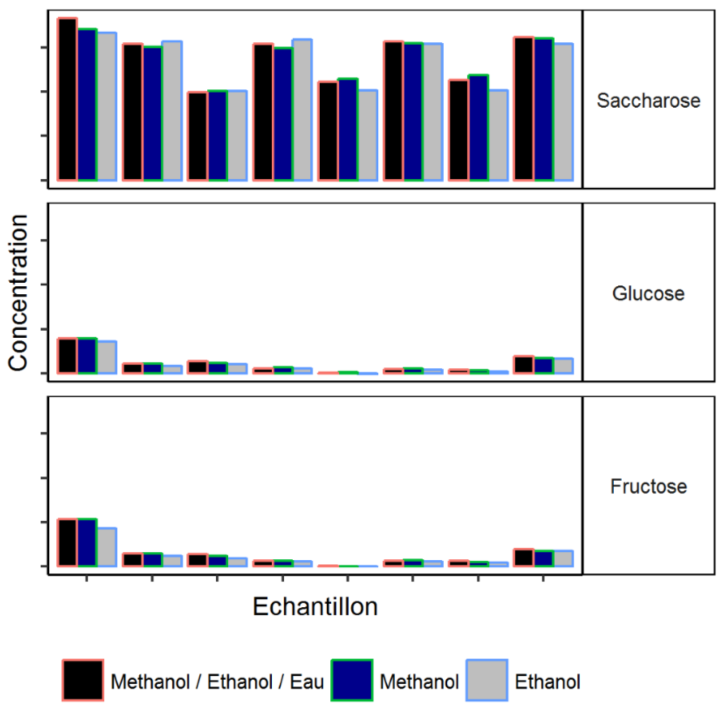
## ANNEXE N°3

RESULTATS OBTENUS POUR LE TEST DES TROIS METHODES D'EXTRACTION

I.Comparaison des méthodes d'extractions sur les concentrations d'amidon via la méthode de dosage présentée en annexe ($g.100g^{-1}$ MS)




II.Comparaison des méthodes d'extractions sur les concentrations en sucres solubles via HPLC ($g.100g^{-1}$ MS)



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# LISTE DES FIGURES

change en faveur de l'absorption racinaire (El Zein et al., 2011), la quantité de réserves azotées est à son minimum. La 3ème phase se situe à la fin de la période de croissance, lorsque la quantité de réserves azotées dans l'arbre augmente faiblement jusqu'à la sénescence, c'est le début de la mise en réserve azotée (Staswick, 1994; Stepien et al., 1994). La 4ème phase débute durant la sénescence, l'azote contenu dans la feuille est recyclé (l'appareil photosynthétique est dégradé) et cet azote (sous forme d'acides aminés est alors transporté vers les parties pérennes de l'arbre et stocké sous forme de protéines de réserve (Sauter et al., 1989; Gessler et al., 2004). Enfin, la 5ème phase correspond à la remobilization azotée via la résorption foliaire qui se finit au cours de l'hiver. Durant cette phase, les acides aminés sont progressivement convertis en protéines de réserve (Staswick, 1994; Stepien et al., 1994; Gomez et Faurobert, 2002; Cooke et Weih, 2005; Valenzuela Nunez et al., 2011; Bazot et al., 2013; Gilson et al., 2014).

**Figure II.6** Schéma représentatif des grandes fonctions des cycles carbonés et azotés de l'arbre adapté librement de la thèse d'Angélique Gilson (2015).

**Figure IV.1** Vue du dispositif expérimental en Septembre 2012 (Crédit photos : T.Paul & F.Bonne)

**Figure IV.2** Photographies de la mesure en hauteur (A) et en diamètre (B) d'un arbre du dispositif. Crédit photos : C.Massonnet.

**Figure IV.3** Hauteur (A) et diamètre (B) moyen des arbres de chaque bâche du dispositif en 2013, avant la mise en place des traitements, moyenne + SE, n=168 par bâche.

**Figure IV.4** Etapes de l'installation du système d'exclusion de pluie. Crédits photos : C.Massonnet et P.A Chuste.

**Figure IV.5** Vue satellite du dispositif expérimental avec le toit installé au-dessus de l'ensemble des arbres. Google Maps le 15/03/2017.

**Figure IV.6** Schématisation (A) et photographies (B) d'une branche avant et après une défoliation d'intensité 75%. Crédit photos B : C. Massonnet.

**Figure IV.7** Photographie à gauche de deux arbres, l'un défeuillé à 75% à gauche et l'autre non défeuillé à droite. La photographie à droite montre ces deux mêmes arbres défeuillés. Crédit photos : C. Massonnet.

**Figure IV.8** Photographie du dispositif de suivi de teneur en eau du sol. Crédit photo : J. Levillain.

growth. From 2015, twigs of dead trees were also sampled using the same procedure than living ones.

**Figure V.2.** Seasonal dynamics of the soil Relative Extractable Water during the growing season (REW, A) and the average of pre-dawn water potential of twigs (B) in 8-year-old beech trees since the start of the experiment in control (C), defoliated (D), soil water deficit (Dr.) treatments. Black arrows indicate the dates of the sampling. The dashed line indicate the threshold value of 40% of REW from which the stomatal conductance is impacted according to Granier et al (1999). Different letters means a significant difference ($p<0.05$) between treatments for a given date; mean ± SE, n=8.

**Figure V.3.** Mean height (top, cm) and diameter (bottom, mm) soil water deficit (Dr.) or under defoliation (D), C is for control treatment, i.e well-watered trees and no defoliated in 2014,2015 and 2016. Mean ± SE. Different letters indicate significate difference between treatment for a given date while stars indicate a significate effect of time between 2014 and 2016, n=8.

**Figure V.4.** Mean (±SE) concentration (g.100g-1DM) of starch (black) and total soluble sugars (grey) on twigs from current year of sample (A) and one-year-old twigs (B) on trees from of soil water deficit (Dr.) or under defoliation (D) since the start of the experiment. Current-year branches were only sampled at the end of each vegetative season. C is for control treatment. We sampled dead trees in October 2015 and 2016 and in June 2016. Lower lowercase bold letters indicates differences between treatments for starch concentration, middle italic letters is for soluble sugars and uppercase letters is for total NSC difference. n=8.

**Figure V.5.** Proportion (%) of differentiate sugars on current-year (A) and one-year-old (B) branches from tree under drought (Dr.) or under defoliation (D) or dead trees (Dead) since the start of the experiment, n=8.

**Figure VI.1.** Schematic representation of the 15N labeling experiment. Experimental schedule (top): Four treatments were applied over two years (2014 and 2015) with control (C), moderate (MD) and severe soil water deficit (SD) and defoliation (D) treatments (a 75% removal of the foliage, grey box). One branch per tree was labeled with enriched 15N–urea on one set of trees in spring (LAB 1) and on a second set of trees in summer (LAB 2). Sampling procedure (bottom): At day 0, unlabeled leaves were taken to determine N% and baseline 15N natural abundance. At day 0.5, a set of five leaves was hole-punched, then punched again at day 1, 2 and 4. At day 4, one intact leaf per tree was also sampled to estimate 15N assimilation into foliar proteins. At day 7, another set of five leaves was hole-punched. At day 14, all the leaves and twigs from the labeled branch were harvested. Twigs were analyzed by annual growth unit (Y, Y-1 and <Y-1, where Y is year). In addition, leaves from the apical twigs were sampled to assess the long-distance transport of 15N from the labeled leaves.

**Figure VI.2.** Seasonal dynamics for soil Relative Extractable Water (REW) during the growing season of 2015 (A) in 9-year-old beech trees, and average pre-dawn water potential for twigs at the time of the two labeling experiments (B) at days of year (DOY) 150, 176 and 198 in control (C), defoliation (D) and moderate (MD) and severe soil water deficit (SD) treatments. In A, grey arrows indicate the dates of the two labeling experiments (LAB1 and LAB2) and the dashed line indicates the threshold value of REW below which stomatal conductance is impacted, according to Granier et al., (1999). In B, different letters indicate a significant difference ($p<0.05$) in pre-dawn twig water potential between treatments for a given date; mean, ± SE; n=24.

**Figure VI.3.** Nitrogen (N) concentrations (% DM) in leaves collected on the labeled branches of 9-year-old beech trees in spring (top) and summer (bottom) at days 0.5, 1, 2 and 4 after labeling in the four treatments: control (C), defoliation (D), moderate (MD) and severe soil water deficit (SD). In each season, a set of 12 trees per treatment was used and one branch per tree was labeled. Values are mean ± SE, n=12.

**Figure VI.4.** Dynamics of 15N concentrations (mg.100g-1 DM) in leaves of 9-year-old beech trees in spring (top) and summer (bottom) for 14 days after labeling in the control (C, disc), defoliation (D, triangle), moderate (MD, square) and severe soil water deficit (SD, diamond) treatments. The same five leaves from each labeled branch were hole-punched at days 0.5, 1 and 2. Then, these leaves were harvested at day 4. Five new leaves were then chosen along the labeled branch and were hole-punched at day 7. At day 14, all the foliage remaining on the branch was harvested. The same protocol was applied for both seasons (spring and summer). The effect of time after urea application was calculated only when the same leaves were used from day 0.5 to day 4 (ns: $p > 0.05$, *: $p < 0.05$, **: $p< 0.01$, ***: $p< 0.001$). We tested the effect of season between spring and summer and significant differences were noted “season effect”. Values are mean ± SE; n=12.

**Figure VI.5.** Biomass (A) nitrogen (B) and 15N (C) allocation (%) between leaves and twigs according to annual growth unit (Y. Y-1 and <Y-1, where Y is year) on 9-year-old beech trees 14 days after 15N labeling in spring and summer for the four treatments: Control (C), defoliation (D), moderate (MD) and severe soil water deficit (SD). Values are means ± SE;

n=12. Treatment difference for a given compartment is shown with different letters ($p < 0.05$). Seasonal differences are shown with stars in the summer section (ns: $p > 0.05$, *: $p < 0.05$, **: $p< 0.01$, ***: $p< 0.001$).

**Figure VI.6.** Long-distance transport of 15N (mg.100g-1 DM) from the leaves of labeled branches to the leaves of the apical terminal twigs on 9-year-old beech trees 14 days after labeling in spring (top) and summer (bottom) for the four treatments: control (C), defoliation (D) and moderate (MD) and severe soil water deficit (SD). Different letters indicate significant differences ($p < 0.05$) among treatments for a given date; values are mean ± SE; n=12.

**Figure VII.1:** Schedule of the experiment since the onset of treatments in 2014 (photography 1 and 2). The foliar labeling was made in September 2015 with urea sprayer in a fine mist (photography 3), tree bag was installed before the labeling, remained during the night after labelling then removed the morning after (photography 4). First, we made a harvest one month after the labeling to confirm that the tracer was incorporated in perennial organs via leaf N resorption. Then, harvesting was made at two key phenological dates in February and June 2016. C is for Control, D for Defoliation, MD and SD for Moderate Drought and Severe Drought respectively.

**Figure VII.2.** : Seasonal dynamics of the relative extractable soil water content (REW, A) and the average pre-dawn water potential of twigs (B) in young beech trees during the year 2015 and 2016 in four treatments: moderate soil water deficit (MD), severe soil water deficit (SD), defoliation (D) and control (C). The dashed line (A) indicates the threshold value of REW from which the stomatal conductance is impacted according to Granier et al (1999). The star indicates the labeling time and the two arrows indicate the harvesting times. In B, different letters means a significant difference ($p<0.05$) between treatments for a given date. Mean ± SE, n=8 trees in C and D, 5 in MD and SD in September 2015 and 6 trees in C and D, 3 in MD and SD in June 2016 for pre-dawn water potential of twigs.

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**Résumé :**

Les effets des changements climatiques sur les écosystèmes forestiers sont aujourd'hui mal connus et une augmentation des dépérissements forestiers a été observée ces dernières décennies. La question de savoir comment les arbres vont réagir face à ces changements brutaux est posée par la communauté scientifique mais pas encore résolue aujourd'hui. Plus précisément, les mécanismes écophysiologiques sous-jacents à un phénomène de mortalité sont aujourd'hui mal connus. Néanmoins, la multiplicité des études a permis de dégager plusieurs hypothèses sur les mécanismes fonctionnels mis à l'œuvre lors d'un événement de dépérissement menant à la mortalité dont deux se dégagent : un dysfonctionnement du système hydraulique ou un épuisement des réserves carbonées. Néanmoins, ces hypothèses se sont révélées être non exclusives, ni exhaustives. D'autres hypothèses ont alors été proposées en complément à celles existantes. L'une d'entre elle porte sur la contribution d'un dysfonctionnement azoté lors de la mortalité d'un arbre. En effet, malgré son importance dans la physiologie de l'arbre et son grand investissement dans l'appareil photosynthétique, la disponibilité de l'azote dans le sol est faible ce qui pourrait être préjudiciable pour la survie. L'essence d'étude de ce travail de thèse est le hêtre commun (*Fagus Sylvatica* L.), très présent en Lorraine. De nombreuses observations font état d'un risque potentiel sur l'état écologique du hêtre face à ces changements climatiques globaux par notamment une baisse de la disponibilité en azote du sol et une augmentation des événements de sécheresse. Le travail au sein de cette thèse a donc cherché à évaluer la contribution des métabolismes azoté et carboné aux dysfonctionnements observés lors d'un épisode de dépérissement menant à une mortalité. Afin de mieux comprendre l'importance de ces deux métabolismes, il faut pouvoir modifier la disponibilité de ces deux composants essentiels que sont le carbone et l'azote. Nous avons choisi d'appliquer une défoliation et une sécheresse par un système d'exclusion de pluie dans une expérimentation semi-contrôlée. Une sécheresse modifiera la disponibilité de l'azote dans le sol et réduira l'assimilation carbonée via une fermeture stomatique en réponse à la baisse de la réserve en eau du sol. Une défoliation, quant à elle, par une perte de tissus photosynthétique, va impacter l'assimilation carbonée et mener à une perte d'azote massive étant donnée la forte concentration en azote dans le compartiment foliaire. Durant les 3 ans du projet, nous avons étudié comment le métabolisme azoté et carboné pouvaient être impactés par des défoliations annuelles successives ou une sécheresse longue et intense. Un suivi des réserves carbonées ainsi que des expériences de marquage isotopique ($^{15}N$) ont été réalisés. Notre étude a permis de montrer que face à une contrainte hydrique sévère ou une défoliation, le cycle azoté interne à l'arbre est conservé avec une forte allocation de l'azote vers le compartiment foliaire au printemps et un recyclage efficace de l'azote foliaire vers les organes pérennes à l'automne. Au moyen de marquage foliaire, nous avons pu estimer que cet azote recyclé à l'automne contribue fortement à la mise en place du nouveau compartiment foliaire au printemps suivant et ce, même face à des contraintes importantes. Nous avons pu également mettre en évidence que la quantité de réserves carbonées est maintenue face à une défoliation et, au moins dans un premier temps, face à une sécheresse. Néanmoins, la demande proportionnelle pour des besoins osmotiques a mené à des changements de la composition des sucres de jeunes branches et, face à une sécheresse longue et intense, à une baisse de la quantité de réserves carbonées jusqu'à la mort de l'arbre où les réserves carbonées sont fortement diminuées mais pas totalement épuisées. Finalement, le taux de mortalité dans notre expérimentation fut très faible indiquant la résistance du hêtre lorrain à des contraintes extrêmes que sont des défoliations successives ou une sécheresse longue et intense. Nos résultats soulignent le caractère de résistance du hêtre face à une contrainte via des ajustements des métabolismes internes mais cette résistance pourrait être perdue si la contrainte est plus longue et plus récurrente. Ces éléments peuvent questionner sur le possible maintien du hêtre face aux changements climatiques.

**Abstract:**

The effects of climate change on forest ecosystems are now poorly understood and an increase in forest dieback has been observed in recent decades. The question of how trees will react to these brutal changes is raised by the scientific community but not yet resolved. More precisely, the ecophysiological mechanisms underlying a mortality phenomenon are poorly known today. Nevertheless, the multiplicity of studies made it possible to draw several hypotheses on the functional mechanisms put into action during a death event leading to mortality, two of which emerge: a dysfunction of the hydraulic system or a depletion of carbon reserves. Nevertheless, these assumptions turned out to be neither exclusive nor exhaustive. Other hypotheses were then proposed in addition to existing ones. One of them relates to the contribution of nitrogen metabolism during a mortality event. Indeed, despite its importance in the physiology of the tree and its great investment in the photosynthetic apparatus, its availability in the soil is low which could be detrimental to the survival of the tree if this availability was to decrease. The model genus of this thesis is the common beech (*Fagus Sylvatica L.*), very present in Lorraine. Numerous observations point to a potential risk to the ecological status of beech in the face of these global climate changes, in particular a decrease in the availability of soil nitrogen and an increase in drought events.

The work in this thesis has therefore sought to evaluate the contribution of nitrogen and carbon metabolisms to dysfunctions observed during an episode of dieback leading to mortality. In order to better understand the importance of these two metabolisms, we must be able to modify the availability of these two essential components, carbon and nitrogen. We chose to apply defoliation or drought (not combined) through an experimental experiment on 8-year-old beech trees. A drought changes the availability of nitrogen in the soil and reduces carbon uptake via stomatal closure in response to decreasing soil water availability. Defoliation, by a loss of photosynthetic tissues, impacts the carbon assimilation and lead to a massive nitrogen loss due to the high concentration of nitrogen in the leaf compartment. During the 3 years of the project, we studied how the nitrogen and carbon metabolism could be impacted by successive annual defoliation or a long and intense drought (30 months).

Our study has shown that in the face of severe water stress or defoliation, the first lever of beech to cope with stress is a decrease in growth and leaf area. The internal tree nitrogen cycle is conserved with a strong allocation of nitrogen to the leaf compartment in the spring, its conservation in the foliage during the growing season and an efficient recycling of the leaf nitrogen to the perennial organs during nitrogen winter remobilization. Using foliar isotopic labeling, we have been able to estimate that this recycled nitrogen in the fall contributes significantly to the setting up of the new leaf compartment the following spring, even in the face of significant constraints. We have also been able to show that the quantity of carbon reserves is maintained in the face of defoliation and, at least initially, in the face of drought. Nevertheless, the proportional demand for osmotic requirements in the face of a long and intense drought has led to a decrease in the amount of carbon reserves. When the tree dies, the carbon reserves are greatly reduced, but not until exhaustion, contrary to the theory. Finally, the mortality rate in our experiment was quite low indicating the resistance of the Lorraine beech to extreme constraints such as successive defoliation or a long and intense drought. Our results emphasize the resistance character of the beech against a constraint via internal metabolism adjustments but this resistance could be lost if the stress is longer and more recurrent. These elements can question the possible maintenance of beech in the face of climate change.