Light as a Resource, Stressor and Cue in Mediating Diversity-Productivity Relationships in Forests

Laura Williams[1,1], Raimundo Bermudez Villanueva[2,2], Ethan Butler[2,2], Jeannine Cavender-Bares[1,1], John Couture[3,3], Peter Hajek[4,4], Johanna Klama[4,4], Kyle Kovach[5,5], Christian Messier[6,6], Aboubakr Moradi[7,7], Alain Paquette[8,8], Maria Park[1,1], Peter Reich[2,2], Karen Rice[2,2], Michael Scherer-Lorenzen[4,4], Meredith Schuman[7,7], Artur Stefanski[2,2], Philip Townsend[9,9], and Zhihui Wang[5,5]

[1]University of Minnesota
[2]University of Minnesota Twin Cities
[3]Purdue University
[4]University of Freiburg
[5]University of Wisconsin-Madison
[6]University of Quebec at Montreal UQAM
[7]University of Zurich
[8]Universite du Quebec a Montreal
[9]University of Wisconsin

November 30, 2022

Abstract

In closed-canopy forests, the availability of photosynthetically active light has been a focal point of research, emphasizing the role of light as a resource in limiting carbon assimilation and individual tree growth. However, light shapes the functioning of forest ecosystems through multiple mechanisms. Here, using a series of studies from a network of tree diversity experiments, we explore the multifaceted ways in which light—in terms of both quantity and quality—shapes productivity in mixed-species forests. Spectral reflectance from remote sensing of forest canopies is being increasingly used to detect how tree diversity influences productivity. We demonstrate that airborne imaging spectroscopy captures functionally important differences among canopies related to their structure, chemistry, and underlying biological interactions. Ground-based analyses can show in detail how photosynthetically active light is partitioned among species in mixed-species communities. We show that greater interception of light and greater efficiency of light use, generated by inter- and intra-specific differences, combine to enhance productivity in mixed-species forests. Light may shape forest function not only as a resource but also as a stressor and cue. Plants can perceive light at various wavelengths, use this information to assess their neighborhoods, and subsequently adjust their physiology and allocation. We characterize how light quality—from the ultraviolet to shortwave infrared—varies among and within canopies of differing diversity. We explore how these diversity-light quality relationships arise and connect across levels of biological organization from leaf-level trait expression to forest function. Together these studies lend insight into light-mediated mechanisms that drive relationships between biodiversity and productivity in forest ecosystems—insights that are crucial to predict how biodiversity change will affect future forest function.

Light as a Resource, Stressor and Cue in Mediating Diversity-Productivity Relationships in Forests

Laura Williams[1], Raimundo Bermudez[1], Ethan Butler[1], Jeannine Cavender-Bares[1], John Couture[2], Peter Hajek[3], Johanna Klama[3], Kyle Kovach[4], Christian Messier[5], Aboubakr Moradi[6], Maria Park[1], Alain Paquette[5], Peter Reich[1], Karen Rice[1], Michael Scherer-Lorenzen[3], Meredith Schuman[6], Artur Stefanski[1], Phil Townsend[4], Zhihui Wang[4]

[1]University of Minnesota, [2]Purdue University, [3]University of Freiburg, [4]University of Wisconsin-Madison, [5]Université du Québec à Montréal, [6]University of Zurich

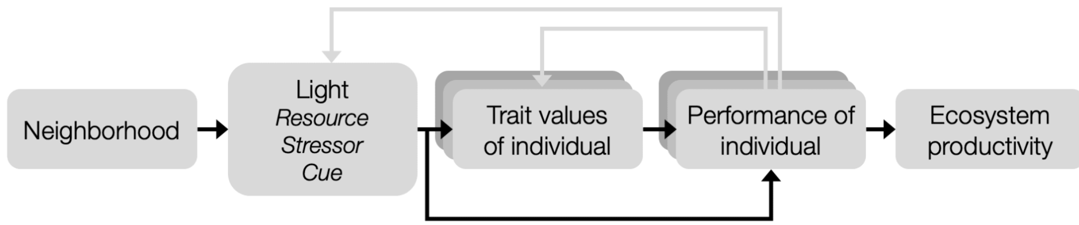
PRESENTED AT:

INTRODUCTION

Multifaceted roles of light in mixed species forests

The availability of photosynthetically active radiation (PAR) limits carbon assimilation and individual tree growth in closed canopy forests.

Here we present a series of studies exploring how a broader consideration of light—from the ultraviolet to shortwave infrared region—may lend insight into the drivers of productivity in mixed-species forests through its multiple roles (1) as a resource, (2) as a stressor, (3) in detection of plant attributes and (4) as a cue to functional responses of plants.



Using a network of field-based tree diversity experiments, we examine:

(1) How light mediates the effect of neighboring tree diversity on leaf trait plasticity.

(2) How light interception and light use efficiency—generated by inter- and intra-specific variation—together drive enhanced productivity in mixed species communities.

(3) How the light reflected from canopies and airborne imaging spectroscopy can detect overyielding in mixed species communities and give insight into its drivers.

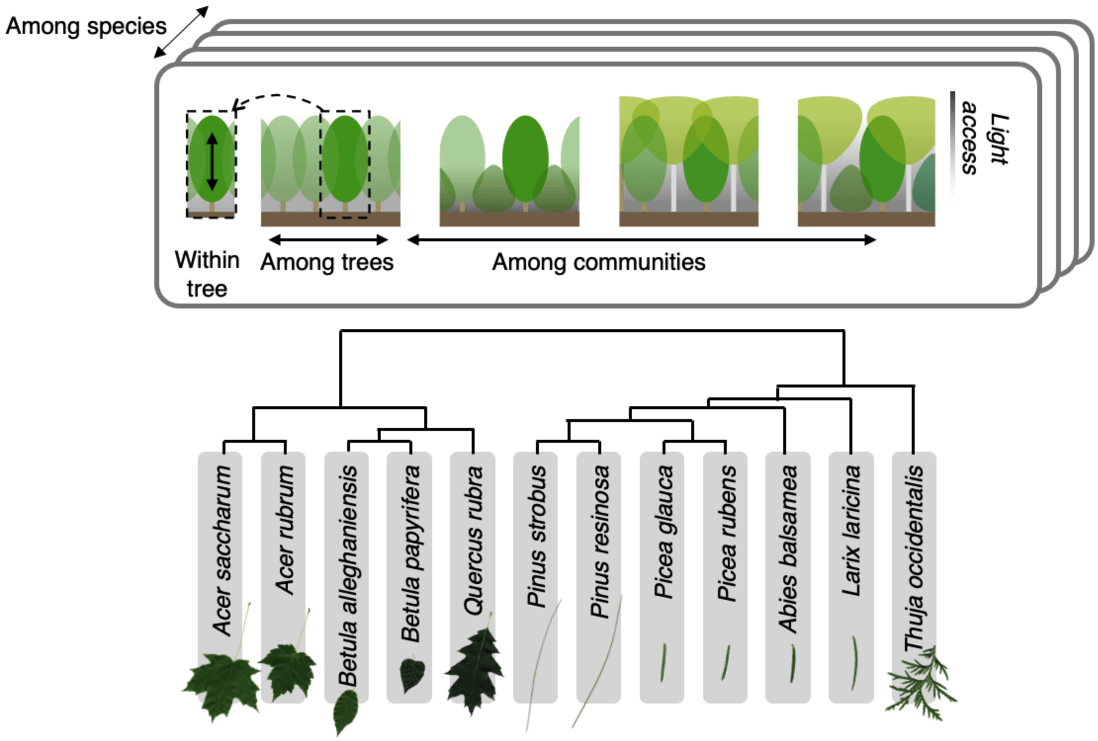
(4) How light quality—from the ultraviolet to shortwave infrared—varies among and within canopies of differing diversity, serving as a cue for plants with consequences from leaf trait expression to forest function.

1. LIGHT AS A RESOURCE

Light mediates community diversity effects on leaf trait expression

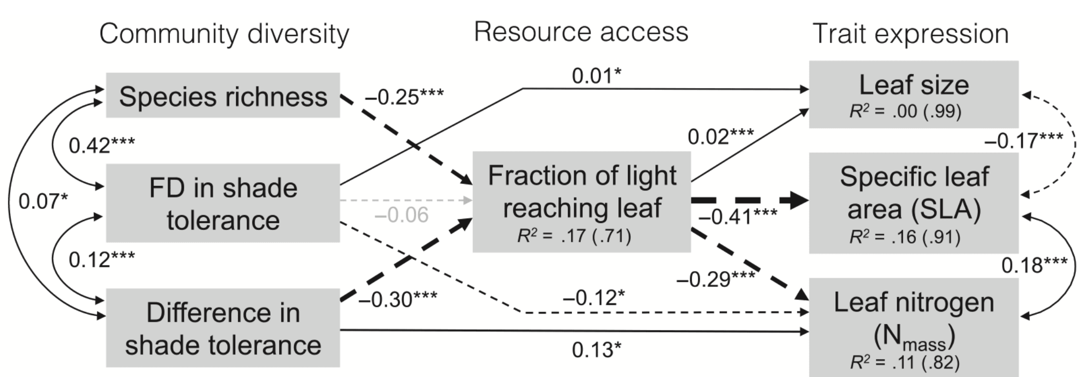
Trait values affect how plants function, with consequences that propagate through scales of ecological organization to affect ecosystem function. Yet trait values can be highly variable both within and among species.

Here we asked if and how community diversity affects leaf trait expression.



At the IDENT-Montreal tree diversity experiment, we examined variation in the leaf trait values of 12 tree species. We characterized trait variation within trees, among trees and among communities, and we assessed the extent to which access to light (specifically, PAR) differed with community diversity to explain observed patterns of trait variation.

We found community diversity affected leaf trait plasticity through its effect on access to light.

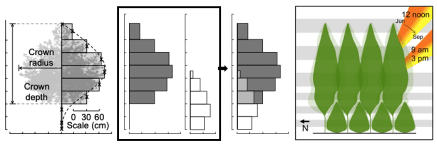


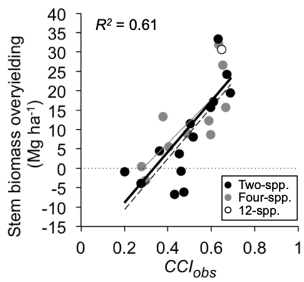
(Williams et al. 2020)

2. LIGHT AS A RESOURCE AND STRESSOR

Crown complementarity, light interception and light use efficiency

Characteristics of tree crowns and how well they fit together to form a forest canopy are key determinants of forest productivity. Crown complementarity—driven both by inherent interspecific differences and neighbor-induced plasticity—contributed to diversity-enhanced productivity across the IDENT-Montreal tree diversity experiment.

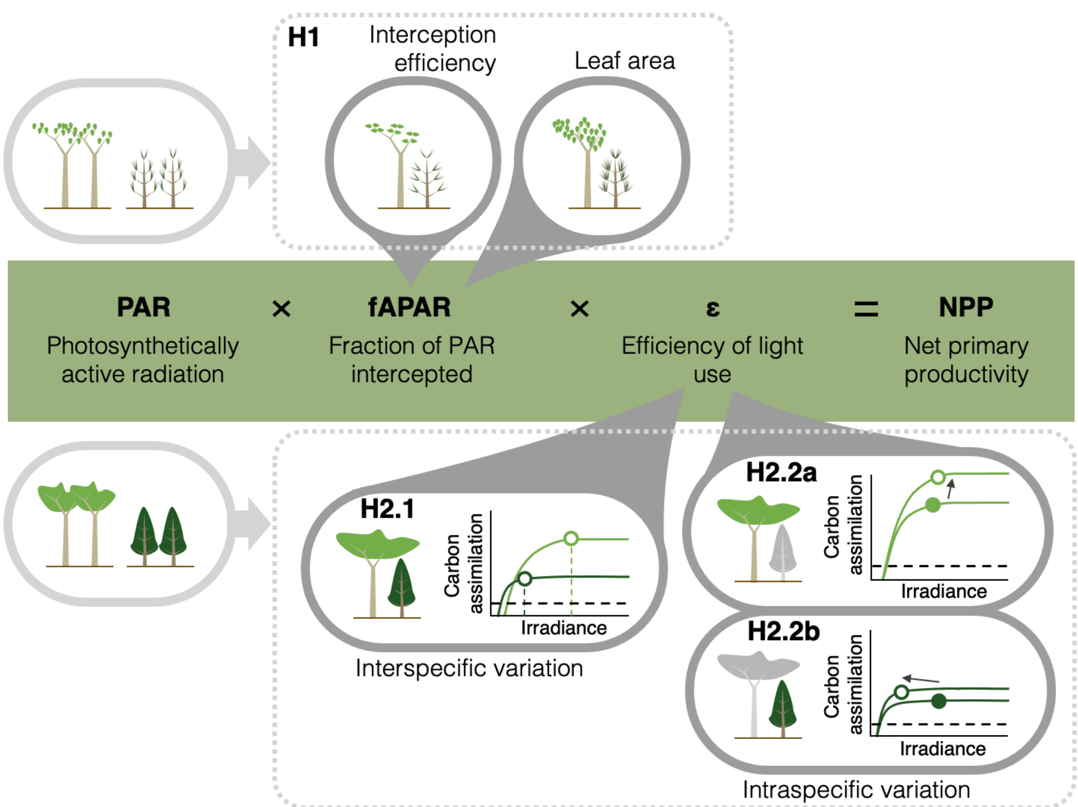




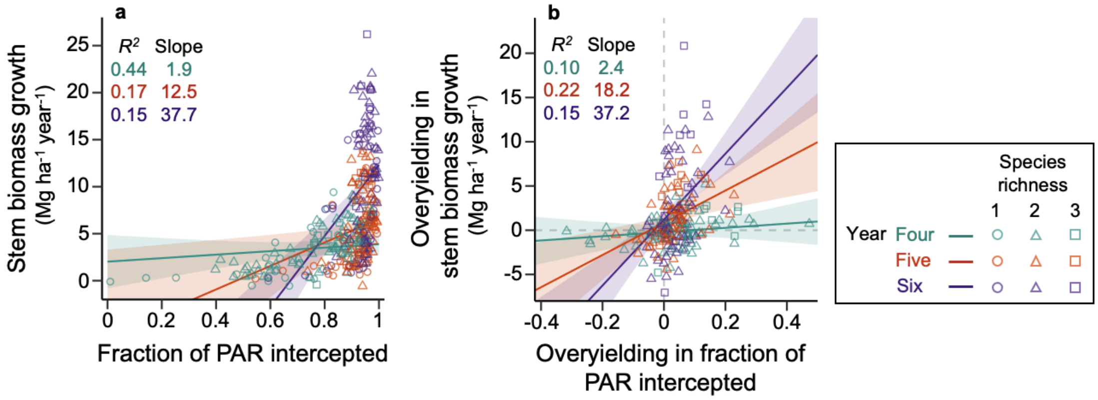
Whether enhanced productivity was attributable to complementary canopies ***intercepting more light and/or using light more efficiently*** was unclear.

Here we assessed whether light interception alone or in combination with the light use efficiency (LUE) of dominant and subordinate species explained patterns of overyielding in 108 young tree communities at IDENT-Cloquet.

Various light-related pathways may enhance productivity in mixed species communities.



We found that mixing species affected species- and community-level light interception, light use efficiency and productivity. Enhanced community-level light interception often, but not always, enhanced productivity and led to overylelding.



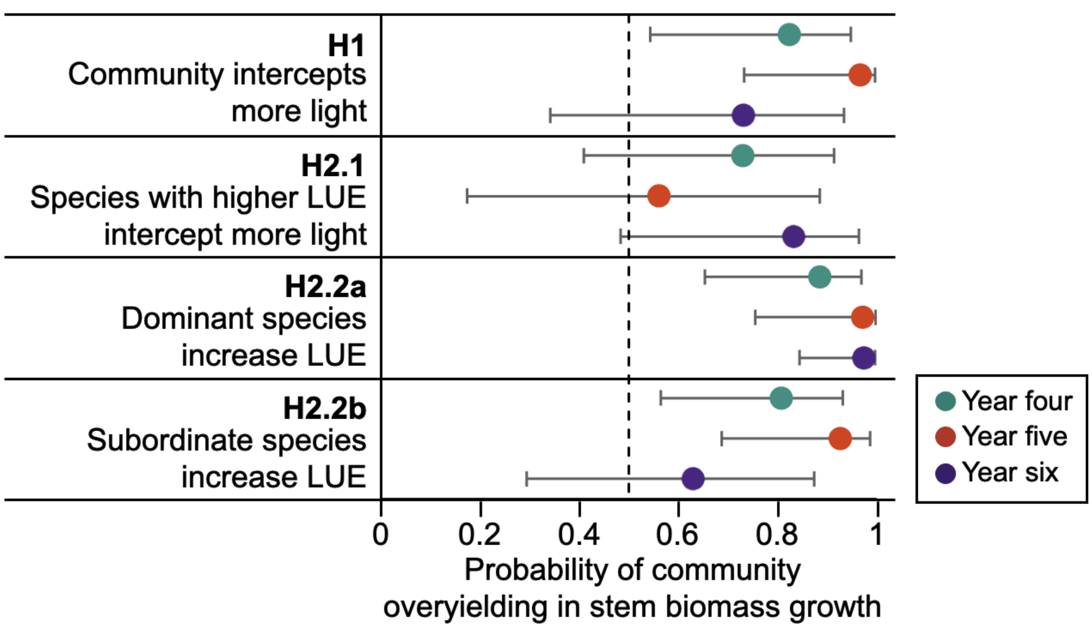
Within mixed species canopies, enhanced community-level light use efficiency occurred in three ways:

(i) species with inherently greater light use efficiency intercepted more light (H2.1);

(ii) dominant species increased their light use efficiency in mixture compared with monoculture such that they grew even more than expected given their increased light interception (H2.2a); and

(iii) subordinate species increased their light use efficiency in mixture compared with monoculture, such that they grew more than expected given their reduced light interception (H2.2b).

When any of these hypothesized pathways were observed, mixed species communities were more likely to overyield.

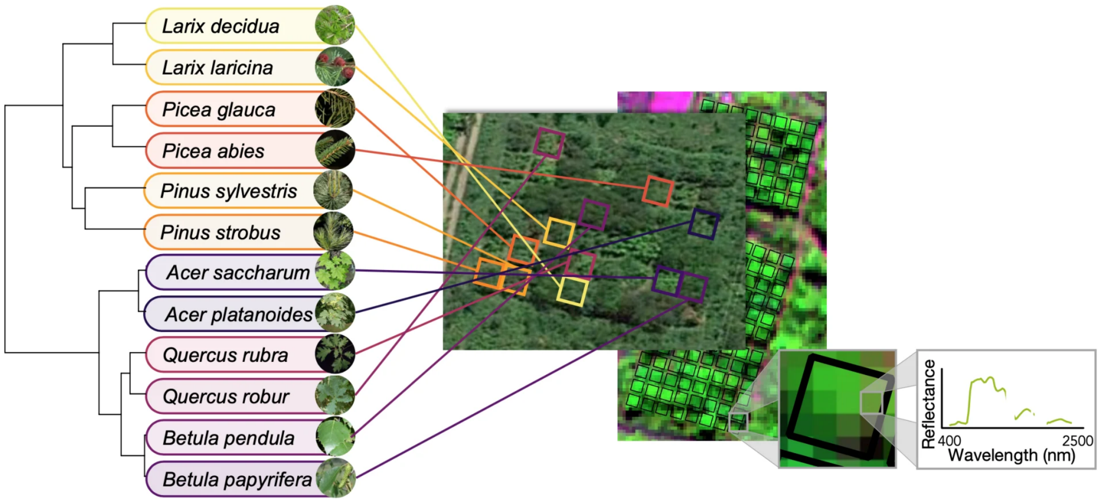


(Williams et al. 2017; Williams et al. 2021a)

3. LIGHT AS A TOOL

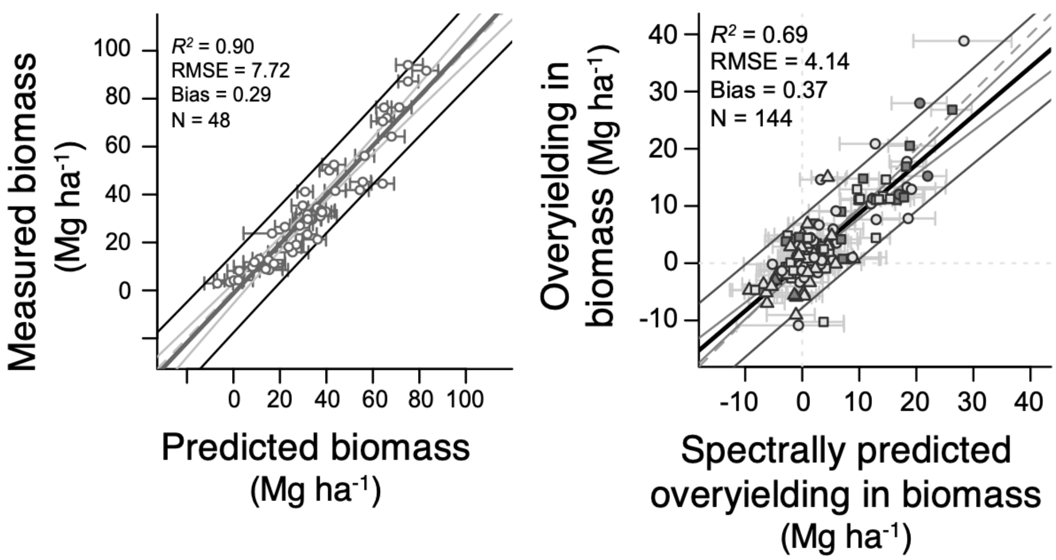
Remote spectral detection of diversity-enhanced productivity

Airborne imaging spectroscopy captures functionally important differences among canopies related to their structure, chemistry, and underlying biological interactions.

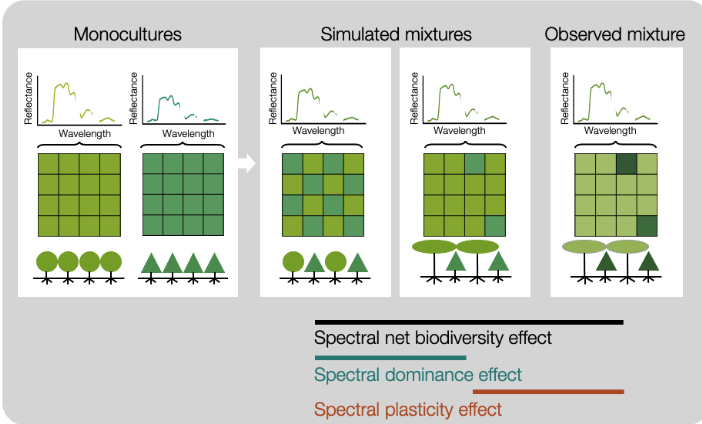


Imaging spectroscopy data (AVIRIS-NG) were collected at the IDENT-Cloquet site, where 12 tree species are planted in monocultures and various mixtures of two and six species.

By comparing spectrally predicted stem biomass in plots of monocultures and species mixtures, we found imaging spectroscopy can detect patterns of diversity-enhanced biomass.



Using spectral trait mapping coupled with a novel spectral partitioning approach, we found overyielding in species mixtures was best explained by species with greater leaf nitrogen dominating the upper canopy, rather than intraspecific shifts in canopy structure or chemistry.



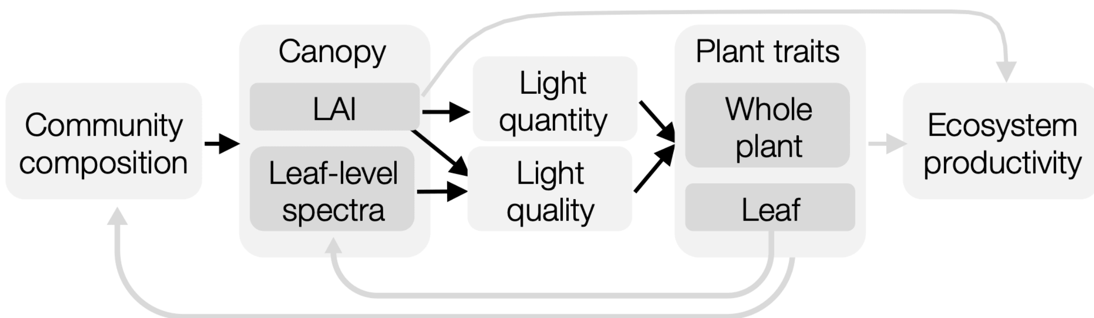
(Williams et al. 2021b)

4. LIGHT AS A CUE

Light quality and diversity effects

Plants perceive light at several wavelengths including in the UV-B, blue, green, red, and far red.

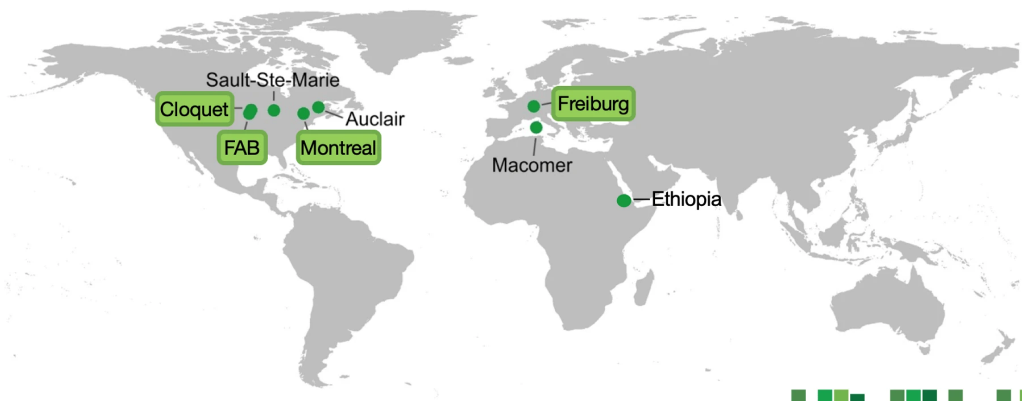
We aim to (1) assess how tree diversity relates to light quality in and below forest canopies at all of these wavelengths known to elicit biological activity in plants, and (2) associate differences in light quality with changes in canopy physiology relevant to explaining plant diversity effects on productivity.



To address these aims, we measured light quantity, light quality, leaf area index (LAI) and leaf optical properties across communities in three tree diversity experiments: IDENT Cloquet and FAB in North America, and IDENT Freiburg in Germany.

APPROACH

The studies we present here used tree diversity experiments that form part of an international network of tree diversity experiments known as IDENT. Each IDENT site includes replicated plots of monocultures and various species mixtures. By using an experimental system that manipulates tree diversity while minimizing environmental variation, we can isolate the effects of tree diversity.



Map of IDENT sites. Those used in this set of studies are highlighted. For more information see https://treedivnet.ugent.be/ExpIDENT.html (https://treedivnet.ugent.be/ExpIDENT.html)

Aerial image of IDENT-Cloquet in August 2021, during the Light Quality fieldwork campaign (Box 4). Credit: Kyle Kovach.

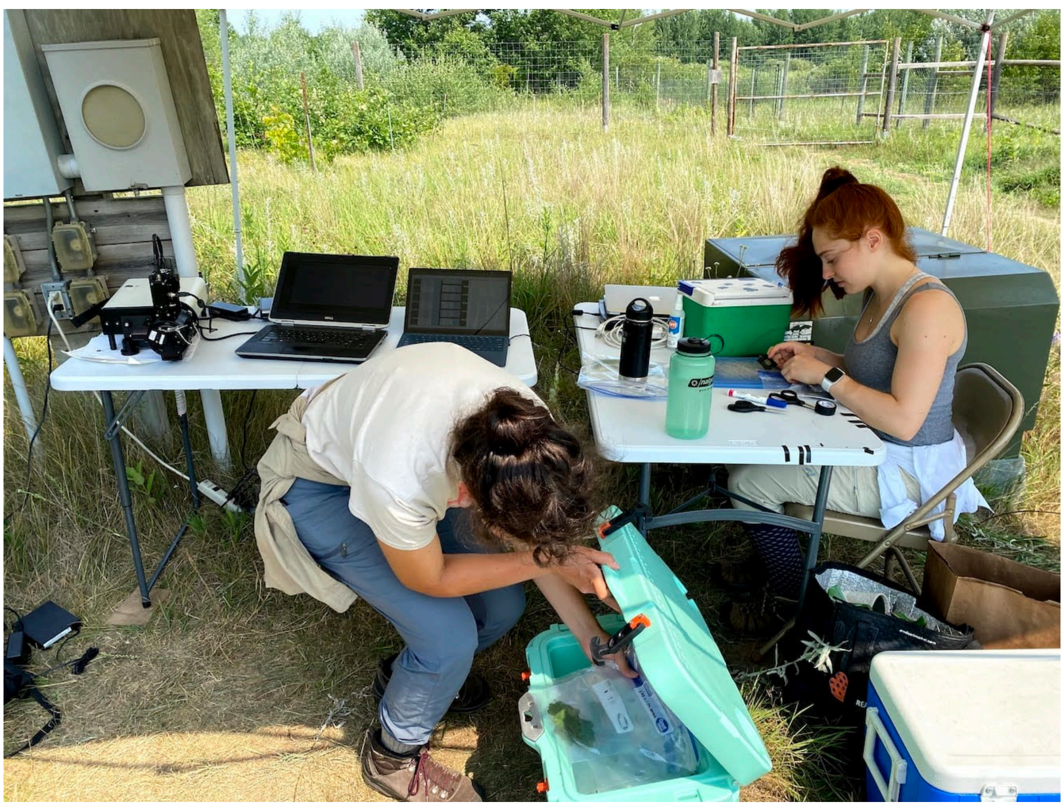
Beneath the canopy at IDENT Montreal in its fourth growing season, during sampling of leaf trait variation (Box 1). Credit: Laura Williams.

IDENT Cloquet in its fourth, fifth and sixth growing seasons (left to right) when light intereption and light use efficiency were assessed (Box 2). Credit: Laura Williams.

Jeannine Cavender-Bares and Aboubakr Moradi measuring irradiance beneath the canopy at IDENT Freiburg, July 2021, to assess diversity effects on light quality (see Box 4). Credit: Meredith Schuman.

Reference irradiance measurements adjacent to the FAB experiment in July 2021 (see Box 4). Credit: Kyle Kovach.

Maria Park, Laura Williams, Raimundo Bermudez, Catherine Glenn-Stone and Artur Stefanski preparing to measure light quality at the FAB experiment in July 2021 (see Box 4). Credit: Kyle Kovach.



Catherine Glenn-Stone and Lauren Latter preparing and measuring reflectance and transmittance on leaf samples at the FAB experiment in July 2021 (see Box 4). Credit: Kyle Kovach.

Artur Stefanski sampling leaves within the canopy at IDENT Cloquet in August 2021 as part of the Light Quality project (see Box 4). Credit: Laura Williams.

CONCLUSIONS

Together these studies illustrate some of the multifaceted roles of light in driving and understanding diversity-productivity relationships in forest ecosystems. These kinds of insights advance our capacity to predict, monitor and manage how biodiversity change will affect future forest function.

For more information, see:

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B. (2017) Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nature Ecology & Evolution* 1, 0063. https://doi.org/10.1038/s41559-016-0063

Williams, L.J., Cavender−Bares, J., Paquette, A., Messier, C., Reich, P.B. (2020) Light mediates the relationship between community diversity and trait plasticity in functionally and phylogenetically diverse tree mixtures. *Journal of Ecology* 108, 1617–1634. https://doi.org/10.1111/1365-2745.13346

Williams, L.J., Butler, E.E., Cavender−Bares, J., Stefanski, A., Rice, K.E., Messier, C., Paquette, A., Reich, P.B. (2021a) Enhanced light interception and light use efficiency explain overyielding in young tree communities. Ecology Letters 24, 996–1006. https://doi.org/10.1111/ele.13717

Williams, Laura J., Cavender-Bares, J., Townsend, P.A., Couture, J.J., Wang, Z., Stefanski, A., Messier, C., Reich, P.B. (2021b) Remote spectral detection of biodiversity effects on forest biomass. *Nature Ecology & Evolution* 5, 46–54. https://doi.org/10.1038/s41559-020-01329-4

We gratefully acknowledge funding from the following sources:

- National Science Foundation's Biology Integration Institutes program (grant no. NSF-DBI-2021898)
- National Science Foundation and National Aeronautics and Space Administration grant awarded to J.C.-B. (grant no. DEB-1342872) and P.A.T. (grant no. DEB-1342778) through the Dimensions of Biodiversity program
- The Canada Research Chairs program
- The Hubachek Wilderness Research endowment, University of Minnesota

AUTHOR INFORMATION

Laura Williams[1 2], Raimundo Bermudez[1], Ethan Butler[1], Jeannine Cavender-Bares[2], John Couture[3], Peter Hajek[4], Johanna Klama[4], Kyle Kovach[5], Christian Messier[6 7], Aboubakr Moradi[8], Maria Park[2], Alain Paquette[6], Peter Reich[1 9 10], Karen Rice[1], Michael Scherer-Lorenzen[4], Meredith Schuman[8 11], Artur Stefanski[1], Phil Townsend[5], Zhihui Wang[5]

[1] Department of Forest Resources, University of Minnesota, Saint Paul, MN, USA

[2] Department of Ecology, Evolution and Behavior, Saint Paul, MN, USA

[3] Departments of Entomology, and Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA

[4] Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany

[5] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

[6] Centre for Forest Research, Universite du Quebec a Montreal, Montreal, QC, Canada

[7] Institut des sciences de la foret temperee, Universite du Quebec en Outaouais, Ripon, QC, Canada

[8] Remote Sensing Laboratories, Department of Geography, University of Zurich, Zurich, Switzerland

[9] Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia

[10] Institute for Global Change Biology, and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA

[11] Department of Chemistry, University of Zurich, Zurich, Switzerland

ABSTRACT

In closed-canopy forests, the availability of photosynthetically active light has been a focal point of research, emphasizing the role of light as a resource in limiting carbon assimilation and individual tree growth. However, light shapes the functioning of forest ecosystems through multiple mechanisms. Here, using a series of studies from a network of tree diversity experiments, we explore the multifaceted ways in which light—in terms of both quantity and quality—shapes productivity in mixed-species forests. Spectral reflectance from remote sensing of forest canopies is being increasingly used to detect how tree diversity influences productivity. We demonstrate that airborne imaging spectroscopy captures functionally important differences among canopies related to their structure, chemistry, and underlying biological interactions. Ground-based analyses can show in detail how photosynthetically active light is partitioned among species in mixed-species communities. We show that greater interception of light and greater efficiency of light use, generated by inter- and intra-specific differences, combine to enhance productivity in mixed-species forests. Light may shape forest function not only as a resource but also as a stressor and cue. Plants can perceive light at various wavelengths, use this information to assess their neighborhoods, and subsequently adjust their physiology and allocation. We characterize how light quality—from the ultraviolet to shortwave infrared—varies among and within canopies of differing diversity. We explore how these diversity-light quality relationships arise and connect across levels of biological organization from leaf-level trait expression to forest function. Together these studies lend insight into light-mediated mechanisms that drive relationships between biodiversity and productivity in forest ecosystems—insights that are crucial to predict how biodiversity change will affect future forest function.