Tree Physiology 24, 1069–1071

Enhancement of understory productivity by asynchronous phenology with overstory competitors in a temperate deciduous forest

WILLIAM M. JOLLY,[1,2] RAMAKRISHNA NEMANI[1] and STEVEN W. RUNNING[1]

[1] *NTSG, College of Forestry and Conservation, SC428, University of Montana, Missoula, MT 59812, USA*

[2] *Corresponding author (mattj@ntsg.umt.edu)*

Received August 6, 2003; accepted January 10, 2004; published online July 1, 2004

Summary Some saplings and shrubs growing in the understory of temperate deciduous forests extend their periods of leaf display beyond that of the overstory, resulting in periods when understory radiation, and hence productivity, are not limited by the overstory canopy. To assess the importance of the duration of leaf display on the productivity of understory and overstory trees of deciduous forests in the north eastern United States, we applied the simulation model, BIOME-BGC with climate data for Hubbard Brook Experimental Forest, New Hampshire, USA and mean ecophysiological data for species of deciduous, temperate forests. Extension of the overstory leaf display period increased overstory leaf area index (LAI) by only 3 to 4% and productivity by only 2 to 4%. In contrast, extending the growing season of the understory relative to the overstory by one week in both spring and fall, increased understory LAI by 35% and productivity by 32%. A 2-week extension of the growing period in both spring and fall increased understory LAI by 53% and productivity by 55%.

Keywords: BIOME-BGC, fPAR, LAI, NPP, phenology, understory.

Introduction

Under the canopy of temperate deciduous forests, some spring ephemerals, shrubs and tree saplings leaf out earlier than the overstory (Gill et al. 1998, Sawada et al. 1999, Houle 2002), on average by about 8 days (Augspurger and Bartlett 2003). Moreover, in the fall, some shrubs and tree saplings delay leaf coloration by more than 2 weeks beyond the time of overstory leaf coloration (Gill et al. 1998). Earlier leaf flush and later leaf senescence by the understory may increase understory productivity when the overstory canopy does not limit irradiance, but the impact of this phenomenon has not been quantified.

Climatic changes have promoted longer growing seasons throughout the world (Myneni et al. 1997, Menzel and Fabian 1999), but few studies have quantified these changes in both understory and overstory phenology. A soil warming experiment showed that both mature trees and understory shrubs leaf out earlier under warmer conditions, but that leaf emergence of saplings is unchanged (Farnsworth et al. 1995). If climatic changes promote novel phenological conditions for the understory relative to the overstory, they could induce significant changes in either stand structure or productivity.

We quantified understory productivity gains that result from earlier leaf flush and later leaf senescence relative to the overstory at Hubbard Brook Experimental Forest, New Hampshire, USA, through modification and application of the ecosystem process model BIOME-BGC. Specifically, we estimated understory and overstory leaf area index (LAI) and net primary productivity (NPP) associated with spring and fall extensions to the growing season to show the impact of asynchronous phenology between the overstory and understory on stratum productivity.

Materials and methods

The ecosystem process model, BIOME-BGC, simulates daily fluxes and storage of carbon, nitrogen and water at specified locations when provided with appropriate weather data, physiographic information and ecophysiological traits of the vegetation (Thornton et al. 2002). We modified the original single-layer leaf model to simulate two leaf layers representing the overstory and understory canopies. Each layer was simulated using identical logic and inputs, with the exception of available radiation, which was reduced for the understory based on the LAI of the overstory leaf layer. Light attenuation by the overstory was calculated according to the Beer-Lambert law (Monsi and Saeki 1953, Campbell and Norman 1998), assuming a light-extinction coefficient for foliage of 0.5 (Chen et al. 1997), and ignoring branch and stem interception.

The BIOME-BGC phenology model predicts leaf flush and leaf senescence as a function of available weather data. The model adequately predicts phenology in temperate deciduous forests throughout the continental USA (White et al. 1997). We modified the original model to allow changes in the predicted leaf flush and senescence dates for each stratum by a specified number of days.

BIOME-BGC simulates a stand-level response and does not require species-specific parameterization. Therefore, we used mean ecophysiological properties appropriate for deciduous broadleaf forests (White et al. 2000) for both the overstory and understory simulations. Model parameter values are based on data for a number of species including dominant species at Hubbard Brook such as *Acer saccharum* Marsh. and *Fagus grandifolia* J. F. Ehrh. (Bormann et al. 1970).

Simulations were conducted with 18 years (1980–1997) of daily climatic data from Hubbard Brook obtained from the DAYMET meteorological archive (Thornton et al. 1997, http://www.daymet.org). In total, five simulation permutations were performed that compared productivity for a synchronized overstory and understory growing season (control) to productivity when the growing season of either the understory or the overstory was extended by either 1- or 2-weeks in both spring and fall. Growing season extensions of this magnitude are within the normal range of growing seasons observed in the field (Gill et al. 1998, Augspurger and Bartlett 2003).

Modeled estimates of daily LAI and NPP (kg C m^{-2} day^{-1} and kg C m^{-2} day^{-1} $year^{-1}$, respectively) for 18 years were made and expressed in absolute units as well as relative to the control. Estimates of LAI from BIOME-BGC for both the overstory and understory were compared with field-measured values of overstory and understory LAI at Hubbard Brook (Rhoads et al. 2002).

Results and discussion

The 18-year, mean predicted growing season length for this site is 184 days. The addition of 7 or 14 days at both the beginning and the end of the growing season represented a total growing season increase of 7.6 and 15.3%, respectively. In both canopy strata, additional growth days allowed more carbon to be fixed relative to the unextended growing season. Some of the additional carbon was allocated to the production of additional leaf area, but the predicted absolute changes in canopy leaf area were relatively minor. When the ends of the growing season were extended by 1 or 2 weeks, maximum overstory LAI increased by only 0.1 and 0.2 above the initial value of 4.55. Likewise, the absolute changes in understory LAI were predicted to increase by only 0.1 and 0.2 above the initial (control) value of 0.45. The latter increases in understory LAI, however, have a large effect on light interception and, thus, NPP, because an increase in LAI from 0.45 to either 0.59 or 0.69 represents an increase in light interception from 22 to 26 or 30%. However, because of the exponential relationship between light interception and LAI, a comparable absolute increase in overstory LAI, from the control value of 4.55, will result in an increase in light interception from a control value of 90% to 90.5 or 91%. These simulated LAI values were within the range of mean field-measured overstory and understory LAI values at Hubbard Brook, i.e., 4.8 ($n = 96$) and 0.7 ($n = 93$), respectively (Rhoads et al. 2002).

Predicted changes in NPP closely parallel the predicted changes in light interception. Net primary productivity for the control overstory and understory averaged 747 and 190 kg C m^{-2} $year^{-1}$, respectively. Extending the growing season by 1 or 2 weeks in both spring and fall increased overstory NPP by only 2 or 4% (776 to 786 kg C m^{-2} $year^{-1}$), but it increased understory NPP by 32 or 53% (251 to 291 kg C m^{-2} $year^{-1}$).

Figure 1 shows the 18-year, mean daily change in overstory and understory NPP as a result of a 1- or 2-week spring and fall extension of the growing season. When overstory canopy duration was extended, the mid-growing season NPP decreased (Figure 1), because the respiration costs of the predicted increases in LAI were not offset by proportional increases in gross productivity. In contrast, when the understory canopy duration was extended relative to the overstory, gross productivity increased, as increased light interception more than offset the increased respiration costs of a greater leaf area. As a result, productivity increased throughout the growing season. Canopy light interception, and thus gross productivity, increases linearly at first and then approaches an asymptote at high leaf area indices, whereas canopy respiration increases linearly with leaf area over the entire LAI range. Thus, depending on the initial leaf area, the net gains in productivity as a result of an increase in leaf area can be quite different. Net carbon gains for both the overstory and understory were higher in the spring than in the fall, which is consistent with field measurements showing a decline in photosynthetic capacity in the fall (Gill et al. 1998).

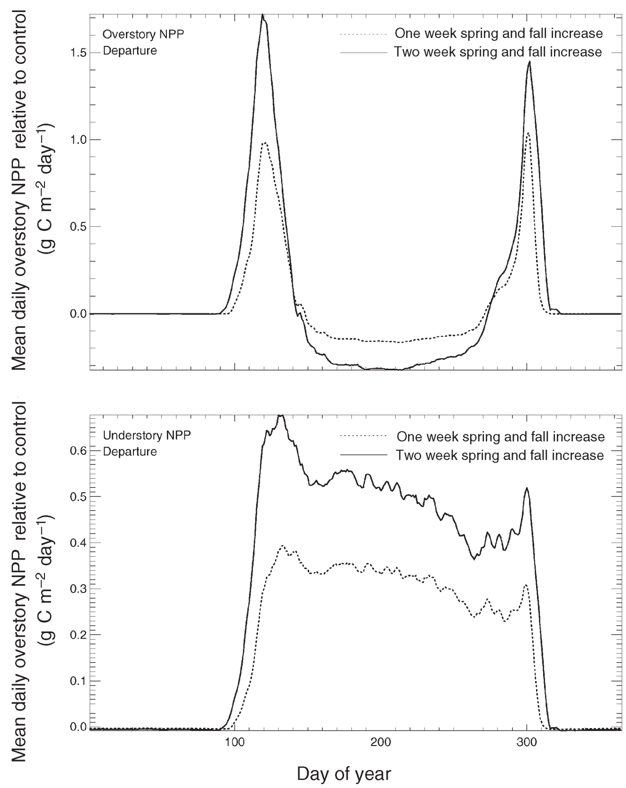

Figure 1. Predicted, 18-year mean changes in daily net primary productivity (NPP) as a result of a 1- or 2-week spring and fall extensions to the growing season of deciduous broadleaf trees grown in the forest overstory (top) and understory (bottom). Dotted lines show predicted changes in NPP resulting from a 1-week extension of the growing season in both spring and fall. Solid lines show predicted changes in NPP resulting from a 2-week extension of the growing season in both spring and fall.

There are two advantages to extending leaf area display in the understory beyond that of the overstory. First, there is minimum competition with the overstory for light during the extended periods of leaf display. Second, by acquiring additional light, a higher LAI can be sustained through the growing season, despite the additional associated respiratory cost. These results suggest that the timing of understory canopy leaf flush and senescence relative to that of the overstory canopy determines variability in understory productivity. If climatic changes create novel combinations of overstory and understory phenology, these differences will impact stand productivity or stand structure.

Acknowledgments

We thank Richard H. Waring and Carl Seielstad for their insightful comments and suggestions on earlier drafts of this manuscript.

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