SEASONAL ACCLIMATION OF PHOTOSYNTHESIS IN EASTERN HEMLOCK AND PARTRIDGEBERRY IN DIFFERENT LIGHT ENVIRONMENTS

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ABSTRACT – The effects of growth light environment on the seasonal acclimation of photosynthetic capacity as well as rates of photosynthesis in the field were investigated in the angiosperm *Mitchella repens* L. (partridgeberry) and the gymnosperm *Tsuga canadensis* (L.) Carr. (eastern hemlock). Irrespective of growth light environment, photosynthetic capacity decreased in winter in partridgeberry but exhibited no seasonal change in eastern hemlock. These acclimatory patterns contrast with previously published results that report strong effects of growth light intensity on seasonal acclimation in another understory angiosperm, *Mahonia repens* (Lindley) Don., and strong wintertime decreases in photosynthetic capacity in a number of gymnosperms. With the exception of eastern hemlock in the exposed site, actual rates of photosynthesis were similar on summer days and on mild days in winter, whereas rates of photosynthesis measured on extremely cold days were much lower. Thus, even within the winter season, daily fluctuations in temperature profoundly affect photosynthesis. The carotenoid pigments that make up the xanthophyll cycle acclimated to winter in a manner that is consistent with their role in the protective process of energy dissipation.

INTRODUCTION

Evergreen plants retain their leaves through the winter season, however, rates of photosynthesis are typically very low during exposure to low temperatures (Logan et al. 1998b, Verhoeven et al. 1999). This is due in part to the limitation imposed by cold temperatures on the activity of the enzymes involved in photosynthetic CO_2 assimilation (Baker 1994, Wise 1995). In addition, seasonal adjustments in the capacity for photosynthesis (the rate of photosynthesis measured at saturating light intensity and optimal temperature) can influence actual rates measured in the field. In the winter, the capacity for photosynthesis generally decreases in coniferous trees, as has been observed in ponderosa pine (*Pinus ponderosa* Laws), Scots pine (*P. sylvestris* L.), blue spruce (*Picea pungens* Englem.), and douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) (Adams and

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Demmig-Adams 1994, Hurry et al. 1998, Verhoeven et al. 1999). The patterns of seasonal acclimation of photosynthetic capacity in angiosperms are more variable. Like conifers, some evergreen angiosperms exhibit decreased photosynthetic capacity in winter (Winter and Koniger 1991, Landhausser et al. 1997, Logan et al 1998b). Others, however, including winter cereal varieties (Huner et al. 1998) and the herbaceous weed *Malva neglecta* Wallroth (Verhoeven et al. 1999), actually increase photosynthetic capacity in winter. Increases in photosynthetic capacity in winter are generally observed in plant species that actively grow during the winter season. Increased photosynthetic capacity in winter is thought to compensate for constraints upon enzyme activities imposed by low temperatures. Logan et al. (1998b) reported that seasonal acclimation of photosynthetic capacity in the broad-leafed evergreen angiosperm *Mahonia repens* was influenced by the nature of the growth light environment. In that study, which was conducted in the eastern foothills of the Colorado Rocky Mountains, it was found that plants growing with year-round full-sun exposure and those that underwent a transition from shade in summer to full-sun exposure in winter exhibited decreased photosynthetic capacities in winter, whereas plants that were deeply shaded year-round maintained similar capacities across seasons. The influence of the growth light environment on the seasonal acclimation of photosynthetic capacity in conifers has not been examined.

Plants growing beneath the canopy of winter deciduous tree species can experience dramatic seasonal changes in growth light environment. The light intensity commonly experienced by understory plants may increase by over two orders of magnitude after leaf drop opens the canopy in autumn. Surprisingly little is known about the response of evergreen understory plants to this change in the light environment (Skillman et al. 1996). Understory plants would need to increase photosynthetic capacity in order to take full advantage of increased light availability for photosynthetic carbon gain. However, mature fully expanded leaves that developed in the shade in late spring/summer may be constrained in their ability to increase photosynthetic capacity (Sims and Pearcy 1992).

In contrast to the enzyme-catalyzed reactions involved in CO_2 assimilation, the process of light absorption by chlorophyll is largely insensitive to temperature (Wise 1995). Thus, during winter, evergreen plants may absorb light energy far in excess of their ability to utilize it via photosynthesis. This is problematic because excessive light absorption can cause the formation of highly reactive forms of oxygen that can damage essential cellular constituents

(Logan et al. 1999). Plants have evolved a means of safely dissipating excess light by converting it to heat, thereby minimizing damage. This process, known as energy dissipation, involves a group of three carotenoid pigments referred to collectively as the xanthophyll cycle (for review see Demmig-Adams and Adams 1996). The xanthophyll cycle is comprised of violaxanthin (V), antheraxanthin (A), and zeaxanthin (Z) and represents a pool of pigments located in the light-harvesting antennae alongside the chlorophylls. Z, and possibly A, are able to facilitate energy dissipation, whereas V is not (Gilmore 1999). Enzymes found in leaves catalyze rapid interconversions among the three pigments of the xanthophyll cycle. Via these interconversions, plants modulate levels of energy dissipation in response to their environment so that excess absorbed light is dissipated without compromising light utilization for photosynthesis. The decrease in photosynthesis that many plants experience in winter results in a reciprocal increase in excess light absorption. Plants have been shown to acclimate to winter by increasing both the overall size of their pool of xanthophyll cycle pigments as well as by converting a greater fraction of their pool to the energy-dissipating forms A and Z (Adams and Demmig-Adams 1994, Logan et al. 1998b, Verhoeven et al. 1999).

The present study examined the influence of forest microsite on seasonal acclimation of eastern hemlock (*Tsuga canadensis* [L.] Carr. [Pinaceae]) and partridgeberry (*Mitchella repens* L. [Rubiaceae]) growing in the Bowdoin Pines in Brunswick, Maine. These species were chosen because they are prominent evergreen gymnosperm and angiosperm members (respectively) of the local flora and they can be found growing across a range of light environments. We sought to determine if eastern hemlock acclimated to winter with a strong seasonal decrease in photosynthetic capacity, as has been observed in other conifers, and also to determine the extent to which growth light environment influenced seasonal acclimation. We also sought to determine if the seasonal acclimatory patterns reported for *Mahonia repens* with respect to growth light environment were also apparent in *Mitchella repens*, a species that occupies a similar niche in northeastern forests. We examined the effects of daily fluctuations in temperature on rates of photosynthesis in the field. Lastly, we measured the seasonal changes in the size and conversion state of the xanthophyll cycle to determine if acclimatory changes were consistent with the proposed role of these carotenoids in the process of energy dissipation.

METHODS

Study Site

This study was conducted in the Bowdoin Pines in Brunswick, Maine (43.914°N, 69.996°W) where eastern hemlock (*Tsuga canadensis* (L.) Carr.]), an evergreen coniferous tree, and partridgeberry (*Mitchella repens* L.), an evergreen angiosperm mat-forming perennial herb, grow natively. Eastern hemlock individuals chosen for this study were between 2 and 3.5 m in height. Plants growing in three microsites (three per species per microsite) were examined: partridgeberry and eastern hemlock growing beneath a thick coniferous evergreen overstory (the 'shaded' microsite); partridgeberry growing beneath a mostly deciduous overstory composed primarily of *Acer* sp. and *Quercus* sp., with some *Abies balsamea* (L.) Miller (the "transitional" microsite); and eastern hemlock exposed to direct full sunlight at the forest edge (the "exposed" microsite). Light intensities were measured *ca.* every 15 minutes from sunrise to sunset at each microsite on a clear day in summer and winter using a quantum radiometer (LI-250, Licor, Lincoln, Nebraska). Light intensities are reported in terms of photon flux density (PFD) in the visible range. We could not locate partridgeberry in exposed microsites sites or eastern hemlock in transitional microsites in the Bowdoin Pines. Field measurements and pigment collections were performed during summer (31 August to 9 September 1999; midday temperatures = *ca.* 24 °C) and on a very cold (18 January 2000; midday temperatures = -11 °C) and a mild day (26 February 2000; midday temperature = 9 °C) in winter. Capacities for photosynthetic oxygen evolution were measured in September 1999 and January 2000.

Rates of photosynthesis in the field

A small percentage of the light absorbed by chlorophyll molecules is re-emitted as fluorescence. The analysis of patterns of chlorophyll fluorescence emission can be used to assess the allocation of absorbed light energy to photosynthesis. Genty et al. (1989) developed a method of using chlorophyll fluorescence to quantify the efficiency with which light energy that is absorbed by the light harvesting antennae associated with Photosystem II of photosynthetic electron transport is used to drive photochemistry (PSII efficiency). PSII efficiency is calculated as $(F_m'-F)/F_m'$, where F_m' is the level of fluorescence emitted from a leaf exposed to a brief flash of saturating light and F is the steady-state level of fluorescence under ambient light. With knowledge of the incident light intensity and PSII efficiency, one can estimate the rate of photosynthesis in terms of the number of photons used to drive photosynthetic electron transport as follows:

Rate of photosynthesis = PSII efficiency X PFD X 0.5

PFD is light intensity in terms of photon flux density (with units of μmole photons m^{-2} s^{-1}) and 0.5 assumes that absorbed light is shared equally between both photosystems of photosynthetic electron transport (Krall and Edwards 1992). This equation yields a slight overestimate of the actual rate of photosynthesis since it does not account for leaf absorptance. Chlorophyll fluorescence emission was measured from attached leaves in the field under ambient temperature and light conditions using a portable pulse-amplitude modulated fluorometer (FMS-2, Hansatech, King's Lynn, Norfolk, UK). Measurements were made at midday.

Photosynthetic capacity

Laboratory-based assessments of gross photosynthetic capacity were made by measuring the rate of oxygen evolution from leaf tissues collected from each site, using a leaf disc gas-phase oxygen electrode (model LD-2, Hansatech, King's Lynn, Norfolk, UK) in humidified 5% CO_2, 21% O_2 and the balance N_2. Leaf temperature was maintained at 25 °C via the use of a circulating water bath. Horizontally oriented, mature leaves were collected randomly from each of the sites in summer and winter. Leaves were wrapped in moist paper towels and immediately transported to the lab. Leaf discs (partridgeberry) or needle tissue of known area (eastern hemlock) were placed in the electrode chamber and exposed to progressively increasing light intensities for an overall period of *ca.* 20 minutes until the measuring intensity of 1700 μmole photons m^{-2} s^{-1} (saturating light) was reached. Measurements were made after leaves had achieved steady state and rates of oxygen production were linear. Respiratory oxygen consumption was measured by darkening the leaf. Gross photosynthetic capacity was calculated as the sum of net photosynthetic oxygen evolution and respiratory oxygen consumption.

Xanthophyll cycle pool size and conversion state

Mature, horizontally oriented leaf tissue was collected from each site at midday in summer and on very cold days in winter. Tissues were immediately frozen in the field in liquid nitrogen and stored under those conditions until analysis of pigment composition by high performance liquid chromatography. Samples were extracted in a combination of 80% and 100% acetone according to Adams and Demmig-Adams (1992) and quantified using a reverse-phase C-18 column according to Thayer and Björkman (1990).

Statistical analyses

Analyses of variance (ANOVAs) and t-tests were performed to determine the statistical significance of differences between microsites and seasons for various parameters. Small sample size diminished the power of our statistical analyses, therefore the most profound, seasonal, or light environment effects are emphasized in the discussion. All statistical analyses were performed using the program StatView (SAS Institute Inc. 1999, Cary, NC).

RESULTS

Light environment

In both summer and winter, eastern hemlock growing in the exposed microsite regularly experienced prolonged periods where light intensities exceeded 1000 μmol photons m^{-2} s^{-1}. Light intensities reaching plants in shaded microsites were low and relatively constant throughout the day, rarely exceeding 20 μmol photons m^{-2} s^{-1}. Only occasional, brief, low-intensity sunflecks (less than 100 μmol photons m^{-2} s^{-1}) were detected in the shaded microsites. Differences in the intensity of the light

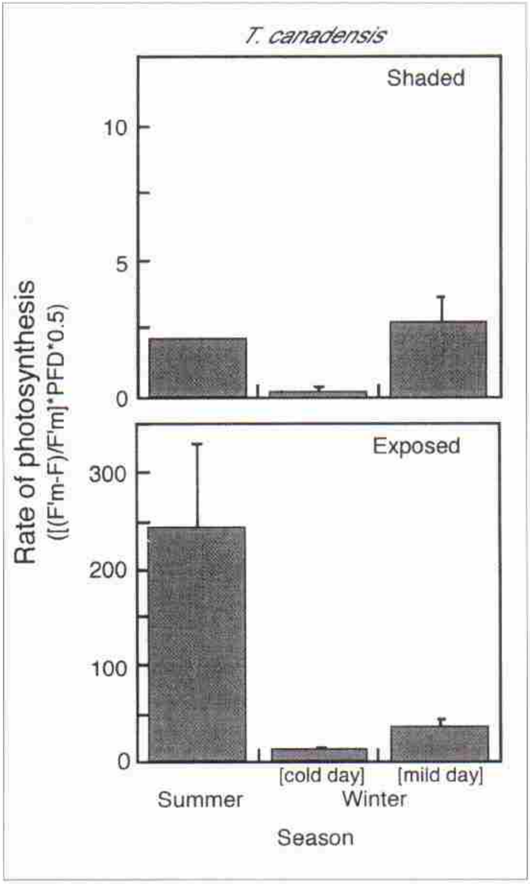

Figure 1. Photosynthetic rates, estimated from chlorophyll fluorescence analysis, of eastern hemlock (*T. canadensis*) growing in deep shade (upper panel) and full-sun exposure (lower panel) in summer (24 °C) and on a very cold (-11 °C) and a mild day in winter (9 °C). Measurements were performed in the field under ambient conditions on clear days. Values are means ± standard deviation; n = 3.

environment between exposed and shaded microsites frequently exceeded two orders of magnitude. The character of the light environment experienced by partridgeberry growing at the transitional microsite underwent a seasonal change as the deciduous overstory trees lost their leaves in autumn. In summer, the light environment at the transitional microsite resembled that of the shaded microsite, with only a single brief sunfleck exceeding 200 μmol photons m^{-2} s^{-1} during the course of a typical clear day. In winter, plants in the transitional microsite experienced exposure to direct full sunlight, with light intensities regularly exceeding 1000 μmol photons m^{-2} s^{-1}.

Rates of photosynthesis in the field

Actual rates of photosynthesis, estimated from chlorophyll fluorescence emission in the field during summer and very cold and mild days in winter are reported in Figures 1 (eastern hemlock) and 2 (partridgeberry). Seasonal patterns in the rates of photosynthesis were similar in shaded

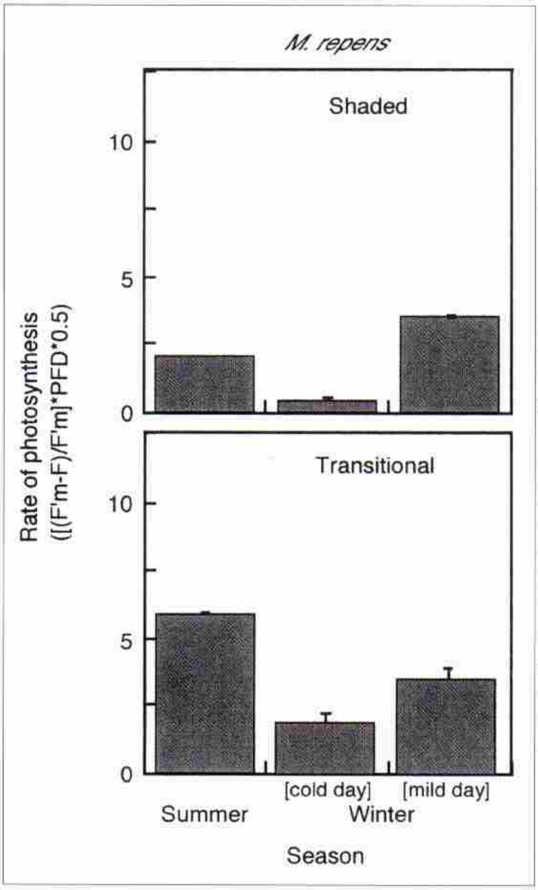

Figure 2. Photosynthetic rates, estimated from chlorophyll fluorescence analysis, of partridgeberry (*M. repens*) growing in deep shade (upper panel) and in a site that undergoes a seasonal transition from shaded to exposed (lower panel) in summer (24 °C) and on a very cold (-11 °C) and a mild day in winter (9 °C). See the Methods for a full description of the growth light environments. Measurements were performed in the field under ambient conditions on clear days. Values are means ± standard deviation; n = 3.

partridgeberry and eastern hemlock. Rates of photosynthesis were low in both seasons (less than 10 μmol photons m^{-2} s^{-1}), owing to the extremely light-limited conditions of these shaded microsites. In both plant species in shaded microsites, the highest rates of photosynthesis were measured on mild days in winter (the difference was statistically significant in partridgeberry, $P < 0.05$). Enhanced albedo due to snow cover and greater light penetration due to the low sun angle lead to slightly increased light intensities at shaded microsites in winter, which account for the greater rates of photosynthesis on mild winter days. During cold winter days, both plant species sustained significant depressions in PSII efficiency, which resulted in rates of photosynthesis that were near to zero and significantly lower than at other measurement times ($P < 0.05$ for both species).

Rates of photosynthesis in eastern hemlock were much greater in the exposed versus the shaded microsite (Fig. 1). Exposed eastern hemlock underwent the most dramatic seasonal change in photosynthetic rate, decreasing approximately five-fold when rates measured in summer and

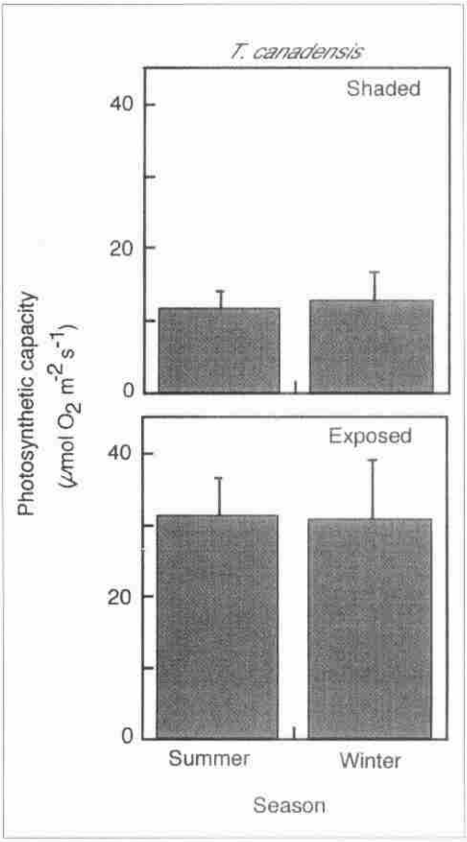

Figure 3. The capacity for photosynthetic oxygen evolution of eastern hemlock (*T. canadensis*) growing in deep shade (upper panel) and full-sun exposure (lower panel) in summer and winter. Values are means ± standard deviation; n = 3.

mild winter days were compared. Within the winter season, the rate of photosynthesis on a cold day was less than half that measured on a mild day, although this difference was not statistically significant.

In summer, rates of photosynthesis were less than 10 μmol photons m^{-2} s^{-1} in partridgeberry growing in the transitional microsite. The differences between the shaded and transitional partridgeberry in rates of photosynthesis in summer can be attributed to the slightly more intense light environment of the transitional microsite. Despite an increase in the intensity of the light environment of over two orders of magnitude after canopy leaf drop at the transitional site, rates of photosynthesis in winter did not increase and were similar to those measured from partridgeberry at the shaded site (Fig 2).

Photosynthetic capacity

Photosynthetic capacities (measured in terms of oxygen evolution) of eastern hemlock in the exposed microsite were almost three-fold higher than those of shaded eastern hemlock in summer and winter

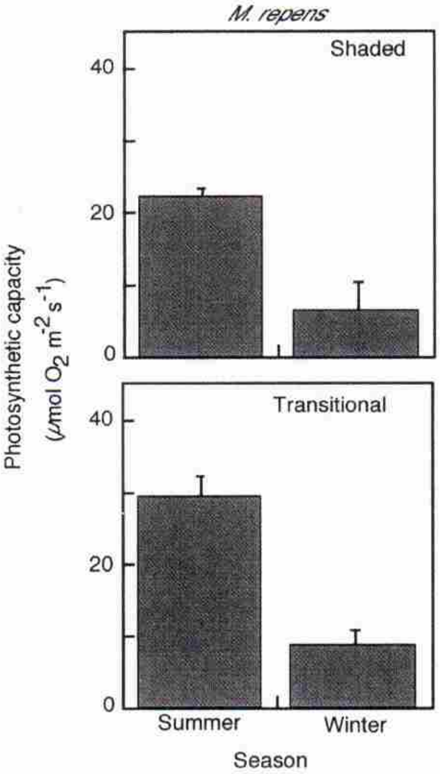

Figure 4. The capacity for photosynthetic oxygen evolution of partridgeberry (*M. repens*) growing in deep shade (upper panel) and in a site that undergoes a seasonal transition from shaded to exposed (lower panel) in summer and winter. See the Methods for a full description of the growth light environments. Values are means ± standard deviation; n = 3.

(Fig. 3; $P < 0.01$ and < 0.05 for summer and winter, respectively). For both shaded and exposed eastern hemlock, there were no significant seasonal differences in photosynthetic capacity.

The photosynthetic capacity of shaded partridgeberry decreased more than two fold from summer to winter (Fig. 4; $P < 0.01$). A similar seasonal trend was observed in the partridgeberry in the transitional microsite (Fig. 4; $P < 0.01$).

Additional measurements of photosynthetic capacity were performed in winter on tissues collected from replicate shaded partridgeberry and eastern hemlock microsites. The photosynthetic capacities of plants at these sites did not differ significantly from those reported in the study (data not shown).

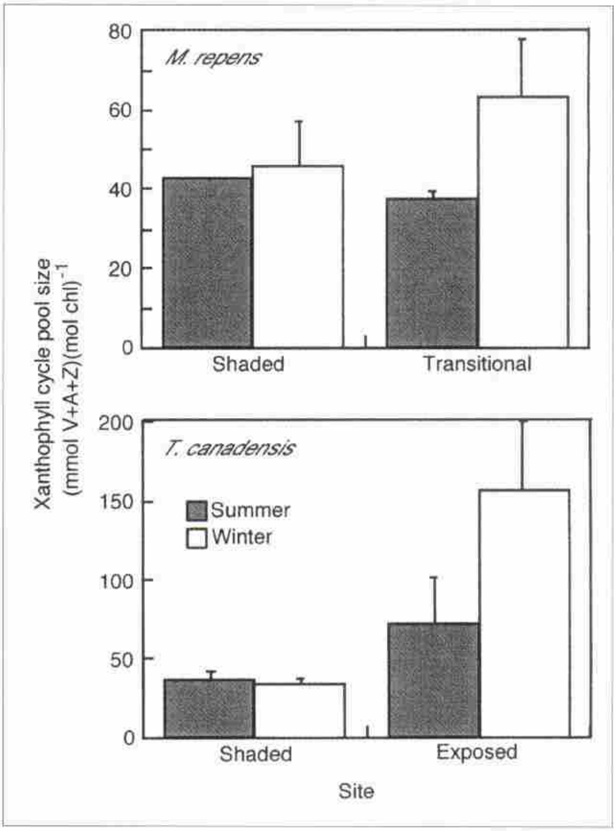

Figure 5. The total xanthophyll cycle pool size of partridgeberry (*M. repens*) growing in deep shade and in a site that undergoes a seasonal transition from shaded to exposed (upper panel) and eastern hemlock (*T. canadensis*) growing in deep shade and full-sun exposure (lower panel) in summer (solid bars) and winter (open bars). Values are means ± standard deviation; n = 3.

Xanthophyll cycle conversion state and pool size

Xanthophyll cycle pool size was approximately 40 (mmol V+A+Z) (mol Chl $a+b$)$^{-1}$ in the shaded partridgeberry and eastern hemlock and did not differ significantly between summer and winter in either species (Fig. 5). During the summer, transitional partridgeberry also maintained a xanthophyll cycle pool size of approximately 40 (mmol V+A+Z) (mol Chl $a+b$)$^{-1}$. Transitional partridgeberry underwent a significant, approximately 60% increase in xanthophyll cycle pool size in winter ($P < 0.05$). Of the plants examined in this study, exposed hemlock maintained the largest xanthophyll cycle pool sizes, with pool size undergoing a significant 100% seasonal increase to over 150 (mmol V+A+Z) (mol Chl $a+b$)$^{-1}$ in winter ($P < 0.05$).

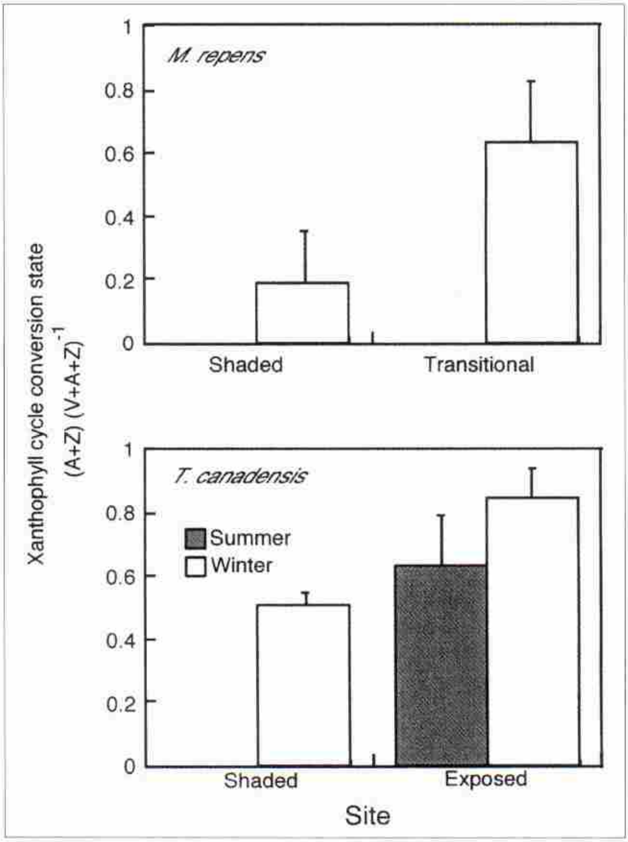

Figure 6. The conversion state of the xanthophyll cycle of partridgeberry (*M. repens*) growing in deep shade and in a site that undergoes a seasonal transition from shaded to exposed (upper panel) and eastern hemlock (*T. canadensis*) growing in deep shade and full-sun exposure (lower panel) in summer (solid bars) and winter (open bars). Values are means ± standard deviation; $n = 3$.

The entire xanthophyll cycle pool was found as violaxanthin in shaded partridgeberry and eastern hemlock and in transitional partridgeberry in the summer, resulting in xanthophyll cycle conversion states of zero (Fig. 6). Mean conversion states for all sites were higher in the winter than summer, with significant increases in transitional partridgeberry ($P < 0.05$) and shaded eastern hemlock ($P < 0.05$). The highest conversion states were found in the exposed eastern hemlock, with mean values above 0.8 in winter.

DISCUSSION

Seasonal acclimation of photosynthetic capacity appeared to be species-specific and not dependent upon the nature of the growth light environment in eastern hemlock and partridgeberry in the Bowdoin Pines. Exposed eastern hemlock maintained significantly greater photosynthetic capacities than shaded eastern hemlock (Fig. 3). This effect of the intensity of the light environment on photosynthetic capacity has been well documented in numerous species (Chow and Anderson 1987; Grace and Logan 1996; Logan et al. 1998a, 1998b). Surprisingly, however, the onset of winter had no effect on the photosynthetic capacity of eastern hemlock at either the exposed or shaded microsites (Fig. 3). As far as we are aware, this is the first study of a coniferous species to report the absence of an acclimatory decrease in photosynthetic capacity in winter. We have no certain explanation for the divergence in the response of eastern hemlock from that of other conifers. This phenomenon merits further examination.

Photosynthetic capacity decreased dramatically in winter in partridgeberry in both the shaded and the transitional microsites (Fig. 4). Therefore, partridgeberry did not exhibit the same patterns of seasonal acclimation as were found for *Mahonia repens* (Logan et al. 1998b), where significant decreases were reported for plants growing in a site qualitatively similar to the transitional microsite but not for deep shade.

We found no evidence to suggest that partridgeberry in the transitional microsite acclimated to seasonal increases in the intensity of its growth light environment in order to enhance carbon gain. Photosynthetic capacities of transitional partridgeberry measured in autumn, a short time after most deciduous leaves had fallen, but before temperatures were regularly below freezing, were intermediate between values measured in summer and winter (data not shown). Despite an increase in incident light intensity on clear days in winter of over two orders of magnitude, partridgeberry in the transitional and shaded microsites maintained similar rates of photosynthesis, as measured by chlorophyll fluorescence analysis (Fig. 2).

It is interesting to note that differences in rates of photosynthesis between mild and very cold days in winter were observed in both species in all microsites (although the difference was not statistically significant in eastern hemlock in the exposed microsite) (Figs. 1 and 2). Clearly, within-season fluctuations in temperature influence the potential for photosynthetic carbon gain in the winter. Plants of both species in the shaded microsites had comparable rates of photosynthesis in summer and on mild days in winter, despite the fact that temperatures on mild days in winter were still substantially below those during summer measurements (Figs. 1 and 2). This indicates that the rate of photosynthesis remained limited by light, and not temperature, in these extremely shaded microsites during warm days in winter. Only during very cold days in winter was this situation reversed and the effect of temperature evident.

Seasonal and site-specific differences in the size and conversion state of the pool of xanthophyll cycle carotenoids were consistent with the role of these pigments in protecting plants against excess light absorption (Demmig-Adams and Adams 1996, Niyogi 1999) (Figs. 5 and 6). Plants protect themselves against damage that can be caused by excess light absorption by invoking the process of energy dissipation, whereby excess absorbed light is safely removed by conversion to heat (Niyogi 1999). It should be noted that the heat generated by energy dissipation does not influence leaf temperature appreciably. Energy dissipation requires the presence of Z or A in the light-collecting pigment beds (Gilmore 1999). The only plants with nonzero xanthophyll cycle conversion states (the fraction of the total xanthophyll cycle pool found as Z and A) in summer were eastern hemlock in the exposed microsite (Fig. 6). This suggests that only those plants were experiencing excess light absorption, which would be expected given that they were exposed to direct sunlight and all other plants were in deep shade in the summer. Plants can increase their Z + A content, and thus their ability to conduct energy dissipation, by increasing the conversion state of the xanthophyll cycle pool and by increasing the overall size of the xanthophyll cycle pool. From summer days to very cold days in winter, plants of both species growing in shaded microsites underwent an increase in the conversion state of the xanthophyll cycle (Fig. 6), but no significant increase in total pool size (Fig. 5). Apparently, the demands for energy dissipation could be met by converting the available pool of pigments. Both partridgeberry at the transitional microsite and eastern hemlock at the exposed microsite underwent increases in both xanthophyll cycle pool size and conversion state from summer to very cold days in winter (Figs. 5 and 6). In winter, these plants were exposed to direct full sunlight and therefore experiencing much greater levels of excess light absorption.

Conclusions

Seasonal acclimation of photosynthetic capacity in eastern hemlock and partridgeberry differed between species and was not sensitive to growth light environment. Overall, the patterns we observed were not consistent with those reported previously, wherein seasonal acclimation in *Mahonia repens* was strongly influenced by growth light environment (Logan et al 1998b) and numerous gymnosperms exhibited strong wintertime decreases in photosynthetic capacity (Adams and Demmig-Adams 1994, Hurry et al. 1998, Verhoeven et al. 1999). Taken together, these findings suggest that it may not be possible to develop broad generalizations about the seasonal acclimation of photosynthesis that are based upon taxonomic affiliation or growth habit. In terms of photosynthetic rate, the greatest fluctuations were often observed when mild and cold days within the winter season were compared. This underscores the dynamic nature of plant responses to cold temperature stress and the importance of characterizing plants across the range of climatic conditions that might be encountered in the field. The size and conversion state of the xanthophyll cycle exhibited patterns of seasonal acclimation that were consistent with the proposed role that these carotenoids play in protecting plants from excess light damage via the process of energy dissipation.

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