

Leaf habit, phenology, and longevity of 11 forest understory plant species in Algonquin State Forest, northwest Connecticut, USA

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Abstract: Many functional attributes of plant species are predicated on their leaf habit. To fully understand the way that plant species coexist and respond to future conditions, it is important to have a thorough understanding of the leaf habit, phenology, and longevity of common forest plant species. I quantified these traits in 11 forest understory species in the Algonquin State Forest of northwestern Connecticut, USA, by labeling and monitoring individual leaves of three replicates of each species over a period of 3 years. While clear patterns exist within the evergreen, wintergreen, seasonalgreen, deciduous, and spring-ephemeral groupings, significant differences exist within and among these groups, including differences in the timing of leafing and senescence, and minimum leaf longevity. Because the impact of local and global disturbance is often predicated on the phenological and life-history traits of species, these differences may be important to the responses that these species have to future disturbance. The size of leaf-supporting structures was positively correlated with leaf longevity across species, supporting a predictive connection between construction costs and leaf longevity. Additionally, the leaf habit of *Oxalis acetosella* L. at this study site is significantly different from that observed previously in the Catskill Mountains, New York State, USA. These differences may be due to local habitat conditions or genetic predisposition.

Key words: leaf habit, leaf construction cost, leaf longevity, leaf phenology.

Résumé : On peut prédire plusieurs attributs fonctionnels des espèces végétales, en se basant sur le port foliaire. Pour comprendre à fond la façon avec laquelle les espèces végétales coexistent et réagiront à des conditions futures, il importe d'avoir une compréhension approfondie du port foliaire, de la phénologie et de la longévité des espèces végétales forestières. L'auteur a quantifié ces caractéristiques chez 11 espèces forestières de sous-bois dans l'Algonquin State Forest du nord-ouest du Connecticut, aux États-Unis, en marquant et en suivant des feuilles individuelles chez trois répliques de chacune des espèces pendant 3 ans. Alors qu'on observe des patrons bien définis au sein des groupes toujours verts, verts en hiver, verts de façon saisonnière, décidues et éphémères printanières, il existe des différences significatives dans et entre ces groupes, incluant des différences dans les moments de foliaison, de sénescence et dans la longévité foliaire minimale. Parce qu'on peut souvent prédire l'impact de perturbations locales ou globales en se basant sur les caractéristiques de la phénologie et du cycle vital des espèces, ces différences pourraient être importantes quant aux réactions de ces espèces à une perturbation future. La dimension des structures qui supportent les feuilles montre une corrélation positive avec la longévité foliaire pour l'ensemble des espèces, ce qui supporte une relation prévisible entre les coûts de construction et la longévité foliaire. De plus, le port foliaire de l'*Oxalis acetosella* L. sur ce site d'étude diffère significativement de celui déjà observé dans les Catskill Mountains, New-York, aux États Unis. Ces différences peuvent être causées par des conditions locales de l'habitat ou par des prédispositions génétiques.

Mots-clés : port foliaire, coût de construction des feuilles, longévité foliaire, phénologie foliaire.

Introduction

There are many links between leaf longevity and leaf function (Reich et al. 1997, 1999; Ackerly and Reich 1999; Westoby et al. 2002; Escudero and Mediavilla 2003; Wright and Westoby 2003). In particular, as leaf life span decreases, photosynthetic and respiration rates increase, nitrogen con-

centration increases, and leaf thickness decreases (Reich et al. 1997, 1999; Westoby et al. 2002). Detailed knowledge of leaf habit (the syndrome of leaf development and loss), phenology, and longevity is therefore useful in predicting the functional traits of plant species. Such information will be valuable in making predictions about species-specific responses to continued high rates of atmospheric deposition (Gotelli and Ellison 2002; Craine et al. 2003; Driscoll et al. 2003) and climate change (Chapin 2003; Shuman et al. 2004; Økland et al. 2004; Houle 2007; Jochum et al. 2007).

While the biodiversity of herbaceous forest understory plant communities is greater than that of other forest layers and their diversity correlates well with the diversity of animal species (Ricketts et al. 1999; Gilliam and Roberts 2003), there is still little understanding of the population

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dynamics and characteristics of leaves of understory plant species (Jolls 2003; Whigham 2004). While descriptions of leaf habit have been made for some understory species (Mahall and Bormann 1978; Uemura 1994), the leaf habits of many species remain unquantified and at least one new pattern has recently been described based on observations of individual leaves (Tessier 2004).

Kikuzawa and Ackerly (1999) hypothesized that leaf longevity would increase among species as the cost of support structures (stem and leaf blade for the purposes of this manuscript) increased. They found that leaf longevity increased in the following order: aquatic plants < annual herbs < perennial herbs < deciduous trees, which supports their hypothesis. The perennial herbs of forest understories, however, include a range of leaf habits (evergreen to spring ephemeral), and their study did not investigate this range within the category of perennial herb.

Plasticity in phenological traits may be important for species coping with a world in which the climate is changing (Peñuelas and Filella 2001; Walther et al. 2002). Making comparisons within a species among locations will help us to understand how individual species respond to different environments and will help to predict which species will survive in various locations in the future, therefore determining the functional characteristics of those ecosystems (Chapin 2003).

The first objective of this study was to document the leaf habit, phenology, and longevity of a collection of herbaceous forest understory species that range in habit from evergreen to spring ephemeral. The goal of this first objective was to examine these leaf properties within and among categories to be used as baseline data for future comparisons and as a means of assessing possible functional differences. The second objective was to compare the size of support structures with leaf longevity among species. The goal of this second objective was to test Kikuzawa and Ackerly's (1999) hypothesis regarding the cost of support structures within the category of perennial herb. The third objective of this study was to compare the leaf habit of *Oxalis acetosella* L. previously documented in a hardwood forest (Tessier 2004) with that in a coniferous setting. The goal of this third objective was to examine the potential for plasticity in leaf habit within a species among locations.

Materials and methods

Study sites

Algonquin State Forest is a transitional plant community between northern hardwoods and central hardwoods in north-west Connecticut (42°00'N, 73°04'W). The most abundant canopy tree species include *Acer saccharum* Marshall, *Acer rubrum* L., *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britton, *Betula lenta* L., *Quercus rubra* L., *Carya cordiformis* (Wangenh.) K. Koch, and *Carya ovata* (Miller) K. Koch. Stands of evergreens are also present, including *Pinus strobus* L. and *Tsuga canadensis* (L.) Carrière. The annual mean temperature is 10.1 °C, the mean January temperature is -3.5 °C, and the mean July temperature is 23.2 °C (NOAA 2007). The annual mean snowfall is 127.0 cm and the annual mean total precipitation is 117.2 cm (NOAA

2007). The rocky soils are from the Charlton–Chatfield complex (NRCS 2007).

The Catskill study site (Tessier 2004) is a northern hardwood forest in the central Catskill Mountains, New York State (41°57'N, 74°31'W). Both the Catskill and Algonquin sites have thin, rocky soils and a mixture of deciduous and coniferous canopy species. The Catskill site, however, receives more annual precipitation (150 cm) and is colder with an annual mean temperature of 5 °C (Tessier 2004). In the Catskills, *O. acetosella* grows under the deciduous trees and in Algonquin it grows mostly under the coniferous trees. The two sites are less than 110 km apart.

Study species

All of the species chosen for this study are herbaceous understory species common to, and abundant in, northeastern forests. Because the abundance of a species is typically correlated with its importance to ecosystem function (Grime 2001), these species are likely to have a strong influence on ecosystem function in the understory and are therefore worthy of study. Leaf habit categories follow Tessier (2004). Evergreen species always have green leaves and those leaves typically survive for more than one year. The evergreen species in this study included *Mitchella repens* L. (Rubiaceae), *Coptis trifolia* (L.) Salisb. (Ranunculaceae), and *Polypodium virginianum* L. (Polypodiaceae). Wintergreen species keep a set of green leaves for one year, replacing the old set in the spring. The wintergreen species in this study included *Dryopteris intermedia* (Muhl.) A. Gray (Aspleniaceae), *Dryopteris marginalis* (L.) A. Gray (Aspleniaceae), and *Polystichum acrostichoides* (Michx.) Schott (Aspleniaceae). Seasonalgreen species have green leaves year round, have a peak in leaf number in the summer, and their leaves are lost and grown throughout the year. The seasonalgreen species in this study was *O. acetosella* (Oxalidaceae). Deciduous species experience a leafless period each year, growing a set of leaves in the spring that abscind in the autumn. The deciduous species in this study included *Trillium erectum* L. (Liliaceae) and *Viola rotundifolia* Michx (Violaceae). Spring ephemeral species expand their leaves before those of canopy trees, and their leaves senesce as the canopy leaves expand. The spring ephemeral species in this study included *Erythronium americanum* Ker Gawler (Liliaceae) and *Claytonia caroliniana* Michx (Portulacaceae).

Field methods

In November 2003, I established the sampling units for each species. For clonal species (*M. repens*, *C. trifolia*, and *O. acetosella*), a 400 cm² plot was delimited around a discrete population and the location of that plot was flagged for future accuracy of sampling. For all other species, an individual plant was chosen and flagged in the field. At the time of sampling unit establishment, all leaves were labeled with an individual number. From November 2003 until November 2006, all sampling units were visited monthly and new leaves were labeled, once elongated from buds. This monitoring provided a record of the month of development of new leaves, the month of senescence of old leaves, and the minimum longevity of all leaves observed on the plants.

Data analyses

To examine the trend in leaf number over time, I graphed the number of leaves of each species during the sampling period. Because leaves were not monitored daily, the actual longevity of each leaf was not known. Minimum leaf longevity is the time from the first observation of a leaf to the last observation of that leaf. I compared minimum leaf longevity among species using an analysis of variance (ANOVA) followed by Tukey's honestly significant difference test at $\alpha = 0.05$, treating each leaf as a replicate. All statistical procedures were carried out using SAS version 8.0 (SAS Institute Inc., Cary, N.C.).

Seasons were defined as follows: Spring included March, April, and May; Summer included June, July, and August; Fall included September, October, and November. Snow cover prevented regular sampling from December through February, therefore, data from those months were excluded from analyses. Production was defined as the number of new leaves observed in a month. Loss was defined as the number of leaves present in the previous month but absent in the current month. Turnover was defined as production plus loss divided by population size in the previous month. I used a 90% confidence interval to determine whether production, loss, production minus loss, or turnover were significantly different from zero in each season, within each species. For these analyses, the three populations of each species were averaged and each year was treated as a replicate.

To test Kikuzawa and Ackerly's (1999) hypothesis relating support structure cost to leaf longevity, I compared the length of the petiole plus leaf blade (based on descriptions from Gleason and Cronquist 1991) with the average minimum leaf longevity among species using linear regression. I then repeated this regression with two outlying species (*M. repens* and *C. trifolia*) removed (see Results).

I performed data analyses comparing data from *O. acetosella* in Algonquin State Forest with data from the Catskill Mountains (Tessier 2004). Minimum leaf longevity was compared between the two sites using a *t* test at $\alpha = 0.05$. Relative leaf production was defined as the leaf production divided by the number of leaves present in the previous month. Relative leaf loss was defined as leaf loss divided by the number of leaves present in the previous month. Relative leaf production, relative leaf loss, production minus loss, and leaf turnover were compared between sites and among months using a 2×8 factorial ANOVA at $\alpha = 0.05$. Because of interactions in all tests, simple effects were isolated by comparing least square means. For this analysis, years were averaged by month and each population was treated as a replicate.

Results

Eight hundred and seventy nine leaves were monitored during this study, including 156 for *M. repens*, 87 for *C. trifolia*, 56 for *P. virginianum*, 82 for *D. intermedia*, 89 for *D. marginalis*, 104 for *P. acrostichoides*, 219 for *O. acetosella*, 27 for *T. erectum*, 32 for *V. rotundifolia*, 18 for *C. caroliniana*, and 9 for *E. americanum*.

Trends in leaf number varied among the life-history categories. Evergreen leaf numbers tended to be the most con-

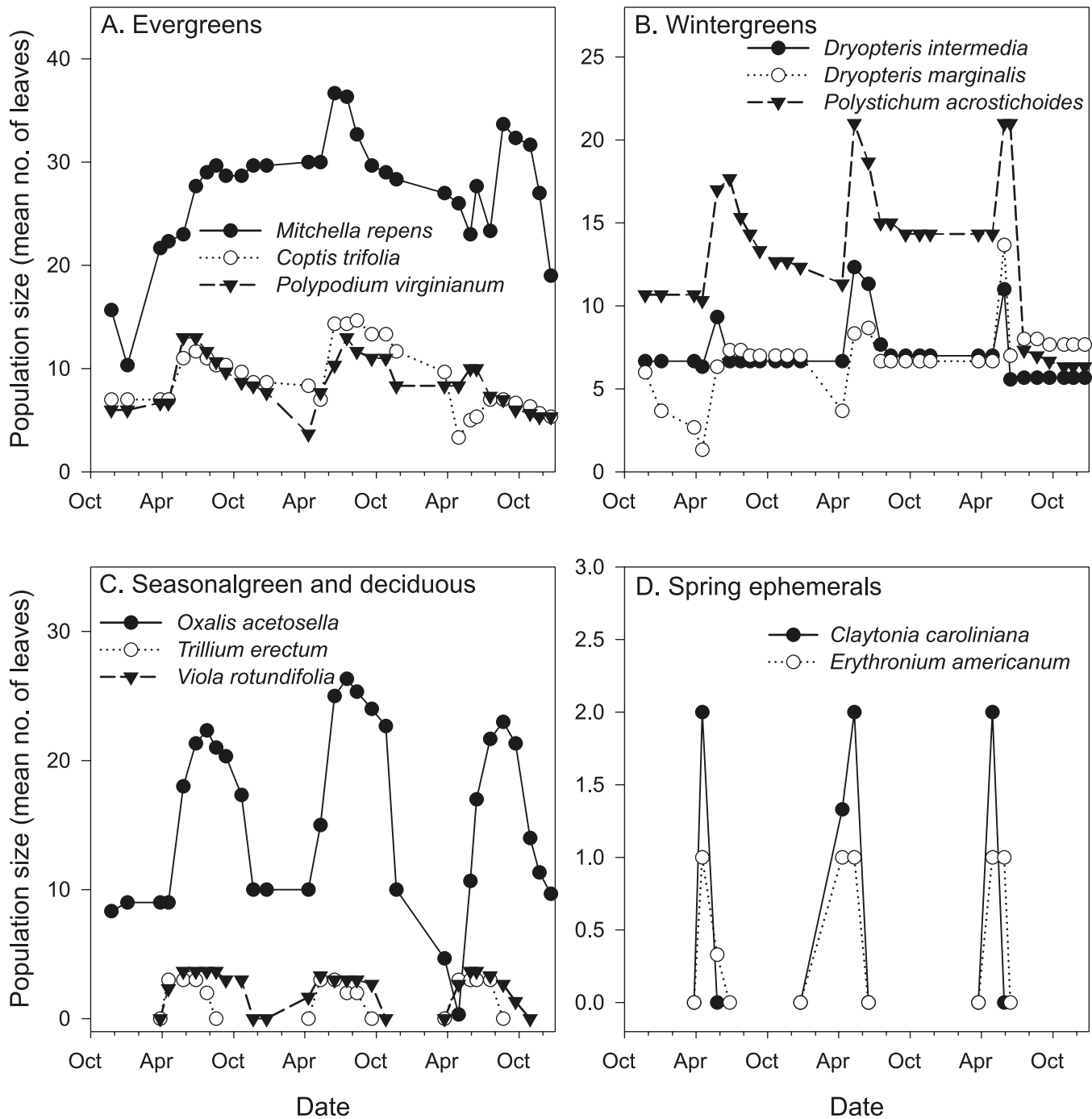
sistent throughout the year (Fig. 1A) with some seasonal fluctuation. Leaf numbers for *M. repens* were the most consistent throughout the year among evergreen species. Wintergreen leaf numbers exhibited a pronounced spike during spring as senescing leaf cohorts overlapped with the development of new cohorts (Fig. 1B). This spike lasted the longest in *P. acrostichoides* (Fig. 1B). Seasonalgreen and deciduous species exhibited a summer peak in leaf number (Fig. 1C). The seasonalgreen species (*O. acetosella*) maintained green leaves throughout the entire year (Fig. 1C). The deciduous species went dormant in the fall and their leaf numbers went to zero each year accordingly (Fig. 1C). Leaf numbers for the spring ephemerals spiked in spring (Fig. 1D) and immediately dropped to zero by summer.

Species differed significantly in their minimum leaf longevity ($F = 28.22$, $p < 0.0001$). There was not a statistically significant difference in the minimum longevity of leaves of evergreen and wintergreen species, and these species had the longest minimum longevities of the species studied (Fig. 2). The spring ephemeral species had the shortest minimum leaf longevities, but those durations were not always statistically different from those of the deciduous species (Fig. 2). This statistical similarity is the result of some short durations in the minimum longevity of leaves of *T. erectum* in the summer of 2004, which led to high variability around the mean. Additionally, leaves of *E. americanum* survived for 2 months of each year, which is not greatly shorter than the longevity of leaves of *T. erectum*. The minimum leaf longevity for *O. acetosella* was not significantly different from the deciduous species nor was it significantly different from *P. virginianum*, the evergreen species with the shortest minimum leaf longevity (Fig. 2).

All of the species except *M. repens* and *C. trifolia* had significant leaf production in the spring (Table 1). *Mitchella repens* had significant leaf production in the summer, but leaf production for *C. trifolia* was so evenly spread throughout the year that there were no seasons of statistically significant leaf production (Table 1). *Oxalis acetosella* had significant leaf production in every season (Table 1). All species except *D. marginalis*, *V. rotundifolia*, and *C. caroliniana* had significant leaf loss in the summer (Table 1). Winter herbivory removed enough leaves from *D. marginalis* that there were not sufficient leaves surviving to result in significant leaf loss during typical periods for other species. Otherwise, rates of herbivory were not important among the species in this study. Leaf loss from *C. caroliniana* was divided between spring and summer among years such that statistically significant leaf loss was not detected. Significant leaf loss during the fall was found for *C. trifolia*, *P. virginianum*, *P. acrostichoides*, *O. acetosella*, and *V. rotundifolia* (Table 1).

Evergreen species had no significant changes in leaf number in any of the seasons (Table 2). Wintergreen leaf number tended to increase in the spring, but decreases differed by species (Table 2). *Dryopteris intermedia* had a significant decrease in leaf number in the summer, but *P. acrostichoides* did not have a significant decrease until the fall (Table 2). The seasonalgreen species had a significant increase in leaf number in the summer and a significant decrease in leaf number in the fall (Table 2). Both of the deciduous species showed a significant increase in leaf number in the spring,

Fig. 1. Population size of (A) evergreen, (B) wintergreen, (C) seasonalgreen and deciduous, and (D) spring ephemeral forest understory species of Algonquin State Forest, northwest Connecticut, from November 2003 to November 2006.



but significant decreases in leaf number differed according to species (Table 2). *Trillium erectum* had a significant decrease in leaf number in the summer, while *V. rotundifolia* did not have a significant decrease until the fall (Table 2). Fast emergence and senescence in *C. caroliniana* during spring prevented me from finding evidence for significant increase or decrease in leaf number among seasons, but leaves of *E. americanum* lived long enough to display a significant increase in leaf number in the spring and a significant decrease in the summer (Table 2).

With the exception of evergreen species and *D. marginalis*, all species had significant leaf turnover in the spring (Table 2). All species except *C. trifolia*, *V. rotundifolia*, and *C. caroliniana* had significant leaf turnover in the summer (Table 2). Only *C. trifolia*, *P. virginianum*, *P. acrostichoides*, *O. acetosella*, and *V. rotundifolia* had significant leaf turnover in the fall (Table 2).

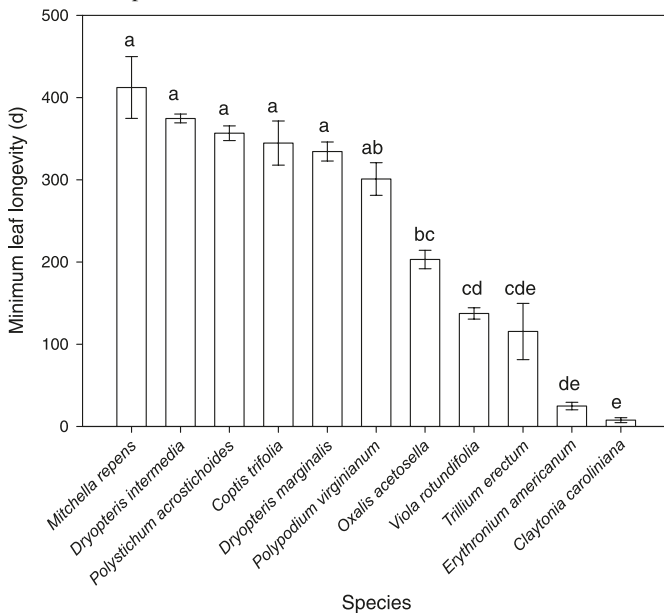
When all species were included, the relationship between the size of supporting structures and leaf longevity was not significantly different from zero ($p = 0.062$; Fig. 3A). With

Table 1. Mean seasonal leaf production and loss (via death or other destruction) among 11 forest understory species in Algonquin State Forest of northwest Connecticut from November 2003 to November 2006.

Species	Leaf habit	Production			Loss		
		Spring	Summer	Fall	Spring	Summer	Fall
<i>Mitchella repens</i>	Evergreen	0.56 (0.40)	11.22 (1.06)*	0.00 (0.00)	1.78 (1.78)	5.33 (1.20)*	3.56 (1.94)
<i>Coptis trifolia</i>	Evergreen	2.78 (1.50)	3.89 (2.67)	0.11 (0.11)	4.22 (3.06)	1.44 (0.29)*	2.11 (0.9)*
<i>Polypodium virginianum</i>	Evergreen	4.66 (1.26)*	2.44 (1.13)	0.00 (0.00)	1.78 (1.31)	3.44 (0.73)*	2.56 (0.48)*
<i>Dryopteris intermedia</i>	Wintergreen	6.22 (0.29)*	0.00 (0.00)	0.00 (0.00)	2.11 (0.99)	4.67 (1.02)*	0.00 (0.00)
<i>Dryopteris marginalis</i>	Wintergreen	6.11 (0.49)*	1.67 (0.67)	0.00 (0.00)	2.33 (1.17)	3.44 (1.83)	0.11 (0.11)
<i>Polystichum acrostichoides</i>	Wintergreen	9.33 (1.45)*	1.89 (0.95)	0.00 (0.00)	2.33 (1.20)	9.33 (2.71)*	1.00 (0.33)*
<i>Oxalis acetosella</i>	Seasonalgreen	9.44 (1.45)*	11.33 (2.34)*	0.55 (0.11)*	4.55 (2.89)	2.78 (0.59)*	13.00 (1.39)*
<i>Trillium erectum</i>	Deciduous	3.00 (0.00)*	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	2.33 (0.67)*	0.67 (0.67)
<i>Viola rotundifolia</i>	Deciduous	3.44 (0.22)*	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.44 (0.29)	3.11 (0.29)*
<i>Claytonia caroliniana</i>	Spring ephemeral	2.00 (0.00)*	0.00 (0.00)	0.00 (0.00)	1.33 (0.67)	0.67 (0.67)	0.00 (0.00)
<i>Erythronium americanum</i>	Spring ephemeral	1.00 (0.00)*	0.00 (0.00)	0.00 (0.00)	0.22 (0.22)	0.78 (0.22)*	0.00 (0.00)

Note: Values are means (\pm SE) from the 3 years of data for three populations of each species ($n = 3$). Values with an asterisk are significantly different from zero based on a 90% confidence interval. Spring includes March, April, and May; Summer includes June, July, and August; and Fall includes September, October, and November.

Fig. 2. Minimum leaf longevity among 11 species of forest understory plants of Algonquin State Forest, northwest Connecticut, based on leaves observed from November 2003 to November 2006. Means with different letters are significantly different at $\alpha = 0.05$. Error bars represent one standard error above and below the mean.



M. repens and *C. trifolia* (two outlying species) removed, however, the relationship was significant and positive ($p = 0.004$; Fig. 3B).

The comparison of *O. acetosella* between the Catskills Mountains and Algonquin State Forest revealed significant differences in leaf longevity and timing of leaf production, leaf loss, change in leaf number, and leaf turnover. Minimum leaf longevity was significantly longer ($F = 167.34$, $p < 0.0001$) in Algonquin (208.12 ± 11.83 d) than in the Catskills (63.91 ± 4.82 d). Leaf production peaked ($F = 3.91$, $p = 0.0003$) in May in Algonquin, but not until June in the Catskills (Fig. 4A). Leaf loss had peaks ($F = 2.25$, $p = 0.0206$) in April and November in Algonquin, but had multiple peaks throughout the year in the Catskills

(Fig. 4B). The only peak in population size ($F = 4.69$, $p < 0.0001$) in Algonquin was a decrease in November, while in the Catskills there was a peak of increase in June and peaks of decrease through late summer and fall (Fig. 4C). Leaf turnover peaked ($F = 8.25$, $p < 0.0001$) in May in Algonquin, but not until June in the Catskills (Fig. 4D).

Discussion

Distinct differences appeared both within and among life-history categories of understory species of Algonquin State Forest in northwest Connecticut. While patterns clearly separated the groups, variability was present within each group.

Leaves of evergreen species commonly survived longer than one year with considerable overlap among leaf cohorts (Fig. 2). Those leaves that had short lifespans often showed signs of damage (animal digging or stepping). The cause of that damage deserves further study. Action by animals may be an important limiting factor in the lifespan of leaves of evergreen understory species. There was little seasonal fluctuation in leaf number throughout the year in evergreen species (Fig. 1; Table 2). This consistency likely speaks to the consistency of the environment in which these species grow (Goldberg 1982), since all of the evergreen species grew under a coniferous canopy except for *P. virginianum*, which had the most variability in leaf number (Fig. 1). Evergreen leaves tended to develop in the spring and summer and to be lost in the summer and fall (Table 1). Turnover in evergreen leaves, therefore, occurred mostly in the summer or fall (Table 2). This pattern suggests that evergreen species prepare for the winter (Chapin 1980; Chabot and Hicks 1982) by producing leaves later in the season than species of other life-history categories (Tables 1 and 2).

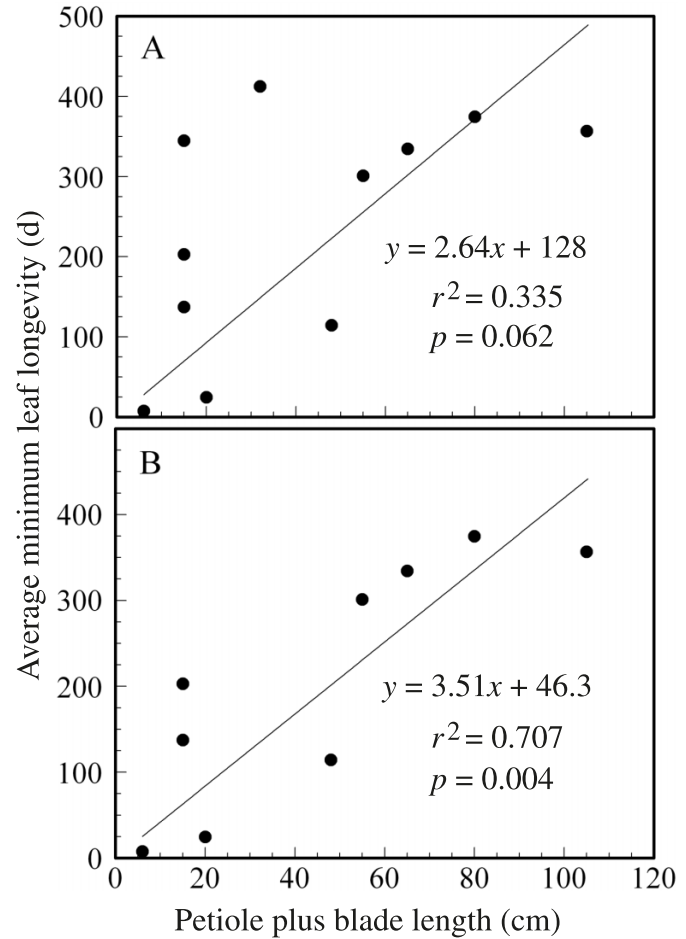
Wintergreen species also had relatively long-lived leaves (Fig. 2). While these species consistently produced their leaves in the spring (Table 1), *P. acrostichoides* kept its leaves into the fall, but the two *Dryopteris* species lost their old leaves in the summer (Fig. 2; Table 1). Leaf number, therefore, spiked in the spring for all wintergreen species, but the spike was longer lived in *P. acrostichoides* than in

Table 2. Mean change in number of leaves of a population (leaf production minus leaf loss) and replacement of leaves (number of new leaves plus number of leaves lost divided by number of leaves in population in previous month) among 11 forest understory species in Algonquin State Forest of northwest Connecticut from November 2003 to November 2006.

Species	Life history	Change in leaf number				Leaf turnover			
		Spring	Summer	Fall	Spring	Summer	Fall		
<i>Mitchella repens</i>	Evergreen	-1.22 (2.08)	5.89 (2.23)	-3.56 (1.93)	0.09 (0.06)	0.60 (0.05)*	0.11 (0.06)		
<i>Coptis trifolia</i>	Evergreen	-1.44 (3.18)	2.45 (2.94)	-2.00 (0.51)	1.15 (0.67)	0.75 (0.32)	0.23 (0.04)*		
<i>Polypodium virginianum</i>	Evergreen	2.89 (2.11)	-1.00 (1.83)	-2.56 (0.48)	1.10 (0.39)	0.55 (0.06)*	0.28 (0.01)*		
<i>Dryopteris intermedia</i>	Wintergreen	4.11 (0.86)*	-4.67 (1.01)*	0.00 (0.00)	1.26 (0.21)*	0.44 (0.08)*	0.00 (0.00)		
<i>Dryopteris marginalis</i>	Wintergreen	3.78 (1.63)	-1.78 (1.97)	-0.11 (0.11)	3.00 (1.49)	0.53 (0.17)*	0.01 (0.01)		
<i>Polystichum acrostichoides</i>	Wintergreen	7.00 (0.88)*	-7.44 (3.63)	-1.00 (0.33)*	1.02 (0.28)*	0.59 (0.07)*	0.09 (0.02)*		
<i>Oxalis acetosella</i>	Seasonalgreen	4.89 (2.60)	8.55 (2.84)*	-12.45 (1.50)*	11.70 (10.58)	0.86 (0.17)*	0.66 (0.02)*		
<i>Trillium erectum</i>	Deciduous	3.00 (0.00)*	-2.33 (0.67)*	-0.67 (0.67)	3.00 (0.00)*	0.89 (0.29)*	0.33 (0.33)		
<i>Viola rotundifolia</i>	Deciduous	3.44 (0.22)*	-0.44 (0.29)	-3.11 (0.29)*	2.59 (0.24)*	0.13 (0.10)	1.26 (0.12)*		
<i>Claytonia caroliniana</i>	Spring ephemeral	0.67 (0.67)	-0.67 (0.67)	0.00 (0.00)	2.61 (0.39)*	0.33 (0.33)	0.00 (0.00)		
<i>Erythronium americanum</i>	Spring ephemeral	0.78 (0.22)*	-0.78 (0.22)*	0.00 (0.00)	1.22 (0.22)*	1.00 (0.003)*	0.00 (0.00)		

Note: Values are means (\pm SE) from the 3 years of data for three populations of each species ($n = 3$). Values with an asterisk are significantly different from zero, based on a 90% confidence interval. Spring includes March, April, and May; Summer includes June, July, and August; and Fall includes September, October, and November.

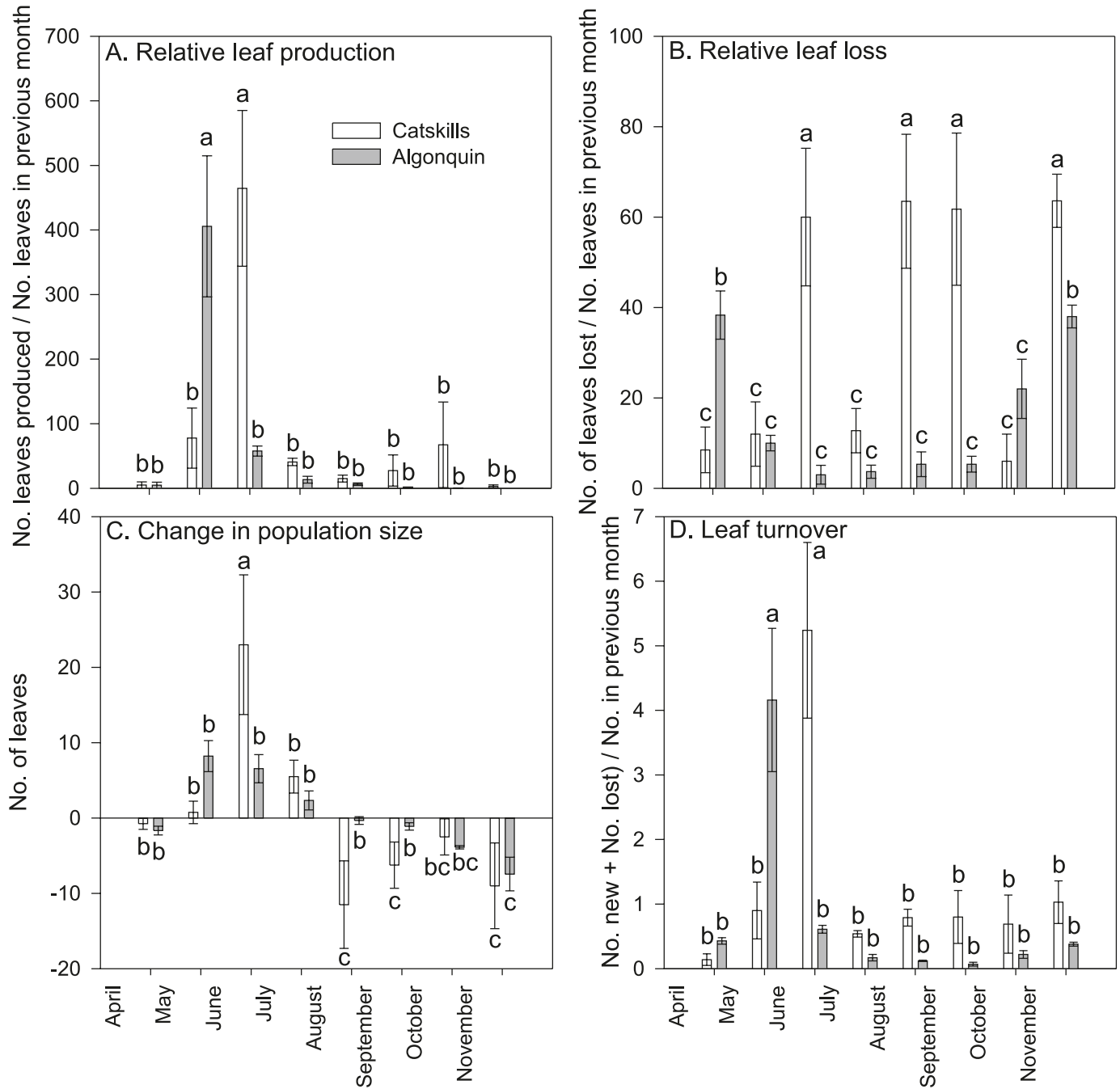
Fig. 3. Positive relationship between support structures and leaf longevity of (A) 11 species and (B) 9 species (excluding outliers *M. repens* and *C. trifolia*) of forest understory plants of Algonquin State Forest, northwest Connecticut.



the *Dryopteris* species (Fig. 1). All wintergreen species exhibited leaf turnover in the summer, but *P. acrostichoides* also had significant leaf turnover in the fall due to later leaf senescence (Table 2). The differences between the *Dryopteris* species and *P. acrostichoides* could have multiple causes. *Polystichum acrostichoides* grows slower than *D. intermedia* (Whigham 2004) and may, therefore, keep its leaves longer to compensate (McKenna and Houle 2000; Escudero and Mediavilla 2003). Alternatively, because *P. acrostichoides* has a more southerly range than the two *Dryopteris* species (Gleason and Cronquist 1991), it may be genetically programmed to keep leaves longer. A future study should compare leaf persistence among species based on their historic range to address this hypothesis.

Oxalis acetosella, the only seasonalgreen in this study, exhibited the characteristic leaf habit of its category (Tessier 2004). This species had multiple, overlapping leaf cohorts each year, a summer peak in leaf number (Fig. 1), year round leaf production and loss (Table 1), summer leaf production (Table 2), and leaf turnover in summer and fall (Table 2). Its leaf longevity was moderate in comparison with the other species (Fig. 2). This documentation of the seasonalgreen pattern in *O. acetosella* at a second study site

Fig. 4. Comparison of (A) relative leaf production, (B) relative leaf loss, (C) change in population size, and (D) leaf turnover of *O. acetosella* in the Catskill Mountains and the Algonquin State Forest. See text for the calculation of these properties. For the Catskills $n = 4$. For Algonquin $n = 3$. Error bars represent ± 1 SE. Means with different letters within a frame are significantly different at $\alpha = 0.05$.



further supports removing this species from its previous consideration as a wintergreen species (Mahall and Bormann 1978).

Deciduous species, as expected, exhibited annual leaf cohorts and subsequently a distinct summer peak in leaf number (Fig. 1). Their leaf longevity was among the shortest of all species (Fig. 2), suggesting a need for high rates of photosynthesis to compensate for a short lifespan (McKenna and Houle 2000). While both deciduous species had spring leaf production and fall leaf loss, leaves of *T. erectum* senesced before those of *V. rotundifolia* in each year (Fig. 1).

The notably short leaf longevity of *T. erectum* in 2004 was probably driven by dry conditions that summer (NOAA 2007) coupled with the species' location on a rocky outcrop. Future studies should examine whether this difference is driven by species location within in a stand (*V. rotundifolia* grew in lower, forest floor settings) or by species specific patterns (Dahlgren et al. 2007). The ability to maintain leaves longer within a growing season may be an important factor in determining fitness in the future when the growing season will presumably be longer than it is today (Hayhoe et al. 2007; Jochum et al. 2007).

The spring ephemeral species displayed their expected, single short-lived cohort each spring (Fig. 1). While both species displayed spring leaf production and early summer leaf senescence (Table 1), leaves of *E. americanum* tended to outlive those of *C. caroliniana* (Fig. 1). The need for cold stratification to promote bud break (Risser and Cottam 1967) and the dependence of leaf development on insolation and temperature in spring ephemerals (Vézina and Grandtner 1965) most likely keeps these species close in their phenologies. Delayed senescence in *E. americanum* relative to that in *C. caroliniana* deserves further study, but may be associated with a trade-off (McKenna and Houle 2000) for a higher cost of leaf production in *E. americanum* due to its large, thick leaves (Reich et al. 1997, 1999; Westoby et al. 2002).

Collectively, the understory species in this study encompassed a wide variety of phenological adaptations, which likely permit them to make use of light, water, and nutrient resources as they become available differentially in the forest. Most species developed new leaves in spring, yet many lost leaves and experienced leaf turnover during the summer (Tables 1 and 2). It may seem counterintuitive to lose new leaves so quickly, but in many cases the plants may be replacing overwintering leaves from the previous year. Differences among species may have important implications as changes in their habitat occur as a result of local and global disturbance.

If leaf longevity is a trade-off between the benefit of photosynthesis from a leaf and the costs of building, maintaining, and supporting a leaf, then the size of supporting structures would be correlated with the longevity of leaves in a species (Kikuzawa and Ackerly 1999). With the exception of two species, the results of this study corroborate the previous findings (Kikuzawa and Ackerly 1999) in support of this hypothesis (Fig. 3). The caution from these data is that some small species may have long-lived leaves. *Mitchella repens* and *C. trifolia* both have relatively small leaves and petioles, but their leaves are leathery (presumably with high carbon and lignin concentrations) and very long-lived (Fig. 2). Therefore, plant size is not a sufficient surrogate for construction and support costs when species vary in cost per unit size. Additional work should investigate the ratios of C:N, lignin:N, C:productivity, and lignin:productivity for these species to further clarify the costs of the production and maintenance of leaves and their support structures to verify that this discrepancy is what prevented *M. repens* and *C. trifolia* from following the hypothesis of Kikuzawa and Ackerly (1999).

While *O. acetosella* has a seasonalgreen leaf habit in Algonquin State Forest, as it does in the Catskills (Tessier 2004), the leaf habit in Algonquin appeared to be more evergreen in nature than that in the Catskills. Algonquin populations had less leaf replacement, longer lived leaves, and less growing season leaf loss than those of the Catskills (Fig. 4). The differences in month of leaf production (Fig. 4) are likely due to differences in climate patterns between the two locations, i.e., spring comes later in the Catskills than in Algonquin. It remains to be determined what drives the differences in leaf habit between the two locations. The differences in phenology within *O. acetosella* between these two populations makes it clear that investigations are needed

to assess the relative importance of genetics and ecological factors in determining the leaf habit of a species. Possibilities include canopy type, biogeochemical cycling, and the genome of the populations. *Oxalis acetosella* grows under hardwood canopies in the Catskills, but is common under evergreen canopies in Algonquin. This difference could also result in biogeochemical differences between the sites. A reciprocal transplant experiment is under way to determine whether plants transplanted to Algonquin from the Catskills conform to the leaf habit of Algonquin populations or if they maintain their Catskill leaf habit and vice versa. Further, populations of *O. acetosella* growing under deciduous canopy in Algonquin have been identified and are part of the reciprocal transplant experiment. In addition, it would be valuable to examine functional patterns among the leaves of these populations to determine whether there are differences in leaf thickness, C:N ratio, or photosynthetic rates. Obtaining this information may be helpful in determining why this species is so successful across the northern hemisphere (Packham 1978) in both deciduous and coniferous forests (Pigott 1990; Amezaga and Onaindia 1997; Onaindia and Amezaga 2000).

In conclusion, there are differences in leaf habit among and within life-history categories of herbaceous understory plant species. Clearly, identifying these patterns and then understanding the functional importance of these differences will be important to predicting future demographics of these populations and the herbaceous communities they make up. The data from this study can be used as baseline data for comparison with patterns that may appear in the future, and can be used as a starting point for quantifying the functional differences among understory species in regard to the way that they acquire resources and cohabitate the understory layer of forests. The size of supporting structures is a valuable tool in estimating leaf longevity across leaf habits, but is not a perfect surrogate for construction costs. Finally, *O. acetosella* is a versatile species in terms of leaf habit. The causes of and properties that permit this plasticity deserve further study.

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