

LEAF LONGEVITY OF *OXALIS ACETOSELLA* (OXALIDACEAE) IN THE CATSKILL MOUNTAINS, NEW YORK, USA¹

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Leaf habit correlates with multiple physiological traits. Understanding ecophysiology is therefore dependent on knowledge of leaf habit. A variety of leaf habits exists within forest understory plant communities. *Oxalis acetosella* is one such understory plant and has long been considered a wintergreen, meaning that it keeps a set of leaves for one full year, replacing them with a new set during spring. To assess the leaf habit of *O. acetosella* and place it into a classification scheme of leaf habits, leaves of four populations of *O. acetosella* were repeatedly censused for two years in a northern hardwood forest of the Catskill Mountains, New York, USA. New leaves developed and old leaves senesced throughout the year, yielding a continual replacement of leaves and a summer peak in leaf number. Leaves that developed in the fall and winter had longer maximum life spans than leaves that developed during the summer. The name “seasonalgreen” is suggested to describe the continual development, senescence, and presence of leaves and annual peak in leaf number within *O. acetosella*. The functional significance of this leaf habit in this species and the possibility of its presence in other species deserve further study.

Key words: Catskill Mountains; common wood sorrel; leaf habit; leaf longevity; northern hardwood forest; *Oxalis acetosella*; understory; wintergreen.

Leaf habit and longevity correlate with a suite of physiological characteristics (Westoby et al., 2002) including photosynthetic rates (Escudero and Mediavilla, 2003), nutrient concentrations (Reich et al., 1999), leaf thickness (Reich et al., 1999), growth rates (Ackerly, 1996), and decomposition rates (Westoby et al., 2002). A variety of leaf habits exists among the herbaceous plants of forest understories (Al-Mufti et al., 1977; Mahall and Bormann, 1978; Uemura, 1994). These leaf habits include evergreens, which keep leaves for multiple years; wintergreens, which keep a set of leaves for one full year and replace them with a new set in spring; and summergreens, which keep leaves only during the growing season. In order to understand the physiological ecology of understory species, it is pertinent to have a complete knowledge of their leaf habits.

Oxalis acetosella L. has long been considered a wintergreen herb (Mahall and Bormann, 1978; Packham, 1978; Grime et al., 1988; Kudish, 1992; Berg and Redbo-Torstensson, 2000; Berg, 2002). During multiple years of vernal field work in the Catskill Mountains of New York State, USA, I did not notice a sweeping replacement of leaves in *O. acetosella* as would be expected of a wintergreen herb. The resulting ambiguity in regard to the leaf habit of this species made it a candidate for learning more about understory leaf habits and thoroughly categorizing leaf habits present in perennial plant species. My objectives were to assess four populations of *O. acetosella* for the growth patterns and longevity of their leaves, place this species into a classification system for perennial plants, and

solidify terminology associated with leaf habit among perennial plant species.

MATERIALS AND METHODS

Study species—*Oxalis acetosella* is a characteristic woodland species (Petersen, 1998; Van Laar and den Ouden, 1998; Lawesson and Wind, 2002) inhabiting the floor of both coniferous and deciduous forests (Pigott, 1990; Amezaga and Onaindia, 1997; Onaindia and Amezaga, 2000) around the northern hemisphere (Packham, 1978). It is low growing, creeping along thin stolons, and displaying three, heart-shaped leaflets. It is considered stress tolerant (Packham, 1978; Packham and Cohn, 1990) because of its ability to tolerate shade, but it cannot tolerate extremely acidic soil (Rodenkirchen, 1992; Økland, 1995; Soukupová and Rauch, 1999; Zerbe, 2002) associated with high rates of atmospheric nitrogen deposition (Pitcairn et al., 1998) and depletion of calcium (Wissemeier and Rodenkirchen, 1994; Rodenkirchen, 1998). It is also not drought tolerant because its populations tend to decline in association with drought (Packham, 1978; Brunet and Tyler, 2000; Tyler, 2001). Part of its ability to tolerate shade is its internal mechanism to exploit sun flecks by focusing light on chloroplasts (Myers et al., 1994). It also produces sun and shade leaves for specialized environments (Packham and Willis, 1977). Producing both chasmogamous and cleistogamous flowers (Eiten, 1963; Berg and Redbo-Torstensson, 2000; Berg, 2002), *O. acetosella* relies heavily on seed production for reproduction (Jankowska-Błaszczuk, 1998; Berg, 2002), but seed production does not seem to limit its spread into secondary woodlands (Verheyen and Hermy, 2001). Congeners exist throughout the world and include other woodland species (Levy and Moore, 1993) and both agricultural crops and weeds (Choudhary and Pathak, 1994; Pütz, 1994; Pearce, 1997; Emshwiller, 2002).

Study site—I conducted this study in a second-growth northern hardwood forest of the Catskill Mountains, New York, USA. The dominant tree species of this forest include *Acer saccharum* Marshall, *A. rubrum* L., *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britton, and *Tsuga canadensis* (L.) Carrière. Dominant understory species of this forest include *Dryopteris intermedia* (Muhl.) A. Gray, *O. acetosella*, and *Huperzia lucidula* (Michx.) Trev., along with seedlings of the genus *Acer*. This stand was last selectively logged in the mid-1900s, and *T. canadensis* was likely harvested for use in the nearby leather tanning industry. Soils are channery silt loam Inceptisols with a well-developed organic layer over relatively thin mineral horizons. Winters in the

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Catskills are cold and summers are moderately cool. The average mean temperature is 5°C. Precipitation is evenly distributed through the year and averages 150 cm/yr.

Field methods—In November 2000, I located four, 100-cm² populations of *O. acetosella* for use in the study (an appropriate quadrat size given the small, clonal nature of this herbaceous understory plant species). These populations were robust, yet isolated enough to minimize edge effect in repeated censusing. I sought to minimize the chance that a leaf would be counted as new when it was in the plot during the current census but outside the plot during previous censuses. I labeled each leaf with a unique number within each population upon establishment of the permanent plots. Subsequently, I recensused the plots periodically from April 2001 to June 2001 and monthly from October 2001 to November 2002 (with the exception of December 2001 to March 2002 when the ground was snow-covered), labeling each new leaf with a unique number at first observance. I also measured the length of each leaflet to the nearest mm at each census from November 2000 to November 2001.

Data analyses—I calculated the total change in leaflet size for each leaf over the measured period and compared the average change to zero using a 95% confidence interval. I graphically compared the size of the four populations over time and the survival of the leaf cohorts over time.

Because only the later censusing was on a regular, monthly basis, I used the data from October 2001 to November 2002 for the following analyses. Also, because log and log + 1 transformations failed to normalize the residuals of the data, I used the nonparametric Kruskal-Wallis test (Conover, 1999) to detect statistical differences among months of origin for leaves at $\alpha = 0.05$. All statistical analyses were performed using SAS version 8.0 (Stokes et al., 2000).

To detect differences in leaf production and senescence among months, I compared the number of new leaves (leaves first observed in the current month) and lost leaves (leaves present in previous month but absent in current month) by month using the four populations as replicates. To detect differences in the change in population size by month, I compared the percentage change in total leaf number among months using the four populations as replicates.

Because leaves developed and senesced between census dates, I did not know the exact date of development and senescence of the leaves. Therefore, for each leaf, I calculated its maximum and minimum longevity. Maximum longevity was from the day after the census before the leaf was first observed to the day before the census in which it was no longer present. Minimum longevity was from the day before the census in which the leaf was first observed to the day after the leaf was last observed.

I calculated the average maximum and minimum longevity for all leaves as well as the range of maximum and minimum longevity. To determine if leaves first observed in different months had different longevities, I compared maximum and minimum longevity of leaves among months of origin using each leaf as a replicate.

RESULTS

A total of 414 leaves was monitored during the census period. The average leaflet length for mature leaves was 9.34 ± 0.27 mm (mean \pm SE). The 95% confidence interval for change in leaflet length was -0.009 ± 0.129 mm (mean \pm 95% confidence interval). Because the range of the 95% confidence interval includes zero (-0.138 to 0.120 mm), the mean change in leaflet length was not significantly different from zero.

The populations reached their greatest size during the summer months and were at their smallest during winter (Fig. 1). New cohorts were present during each month of censusing, and these cohorts senesced throughout the year (Fig. 2).

There were significant differences in the number of new leaves ($t = 22.75$, $df = 7$, $P = 0.0019$) and the number of

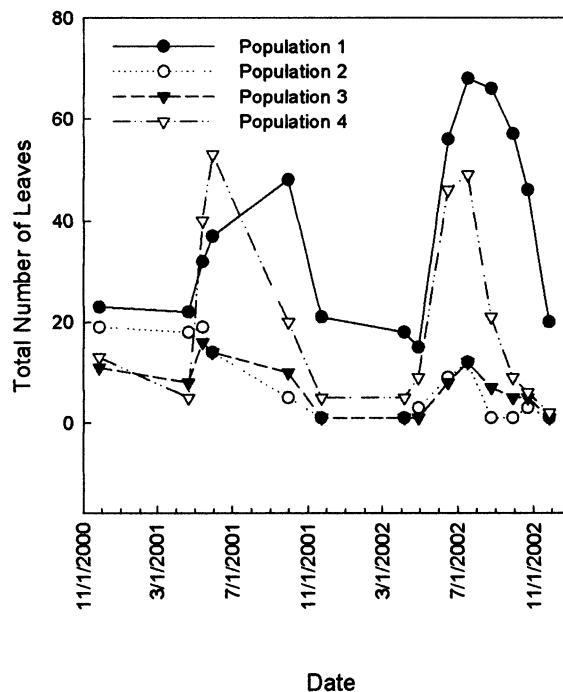


Fig. 1. Size of four populations of *Oxalis acetosella* over 2 yr in a northern hardwood forest of the Catskill Mountains, New York, USA.

lost leaves ($t = 14.83$, $df = 7$, $P = 0.0383$) among months. Presence of new leaves peaked in June (Fig. 3a), and the peak for leaf loss was in August (Fig. 3a). There was a significant difference in percentage change in leaf number among months ($t = 86.14$, $df = 7$, $P = 0.0003$). Relative population sizes increased the most during June and decreased the most during August and November (Fig. 3b).

Maximum leaf longevity ranged from 57 to 394 d. Minimum leaf longevity ranged from 2 to 362 d. The average maximum leaf longevity was 145.6 ± 4.3 d (mean \pm SE), and the average minimum leaf longevity was 63.9 ± 4.8 d. There was a significant difference in the maximum leaf longevity among months ($t = 86.14$, $df = 7$, $P < 0.0001$) but not in minimum leaf longevity among months ($t = 8.56$, $df = 7$, $P = 0.2856$). Leaves first observed during April (leaves produced in very late fall and over winter), October, and November had the longest maximum leaf longevity (Fig. 3c), but there was not a significant difference in minimum longevity among months of origin (Fig. 3c).

DISCUSSION

Oxalis acetosella produces and loses leaves throughout the year with a peak in leaf number during the summer months. The leaves mature quickly and do not change in size once mature. Apparently, resources are put into leaf functioning instead of leaf growth once the leaves are mature.

These results are consistent with the patterns observed by Mahall and Bormann (1978), but yield additional information about leaf longevity in this species. Mahall and Bormann (1978) examined the percentage of leaves that were in any one stage of development throughout the year. They found a large number of new leaves during spring. I found new leaves in spring but also found many new leaves throughout the year. I suggest that Mahall and Bormann (1978) did not see as many

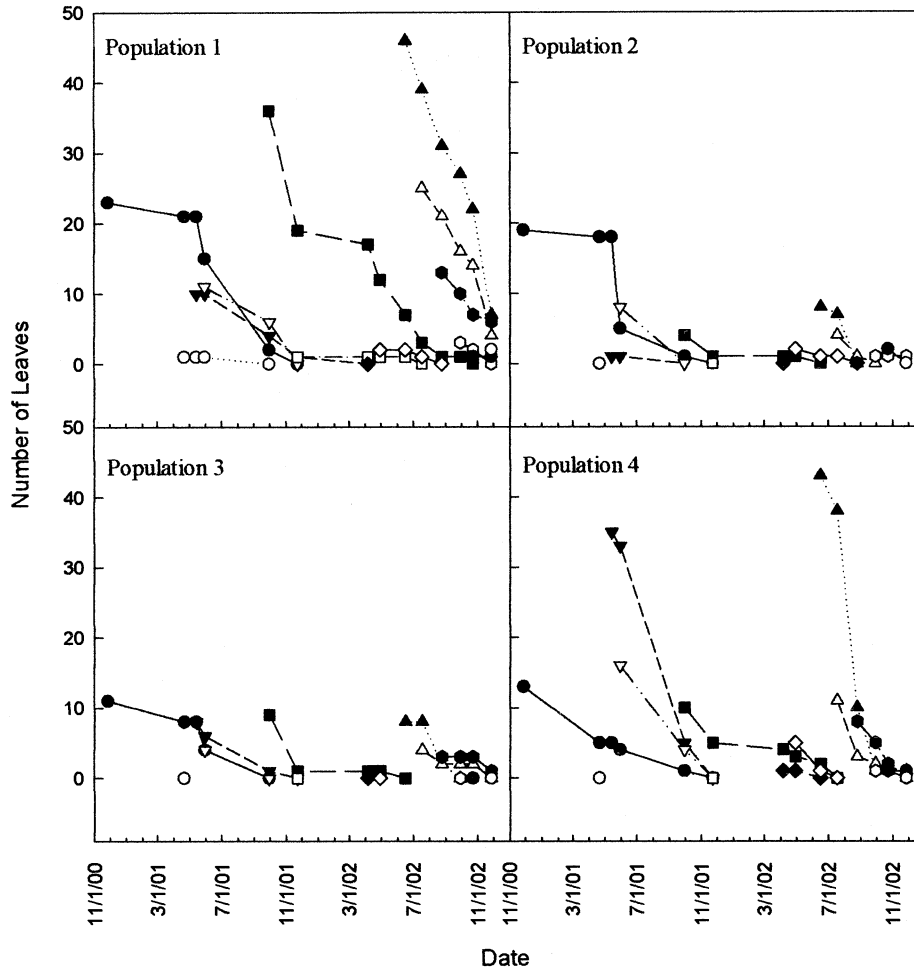


Fig. 2. Size of leaf cohorts over time in four populations of *Oxalis acetosella* over 2 yr in a northern hardwood forest of the Catskill Mountains, New York, USA. Lines originate at the first observation of the leaves. Lines reach zero when there are no longer any leaves present within that cohort.

new leaves during summer due to faster development during warmer months. Cool vernal temperatures would lead to slow leaf development and therefore result in a greater portion of the population being in early stages of development during spring. Warmer summer temperatures would lead to fast development and minimize the time required for a new leaf to fully develop and also minimize the portion of the population that is in early stages of development during summer. Therefore my data do not contradict those of Mahall and Bormann (1978), but they extend our knowledge of the leaf habit of this species and make our understanding more accurate.

The continual production and senescence of leaves throughout the year by *O. acetosella* appears to be rare outside of tropical ecosystems. Recurrent leaf production occurs in some other species, particularly tropical and tundra evergreens as well as wintergreens (Kozlowski, 1971; Jonasson and Chapin, 1985; Hegarty, 1990; Menzel et al., 1993; Barone, 1998; Corlett and LaFrankie, 1998; Osada et al., 2002). Continuous leaf production in tropical tree species is accompanied by equal rates of leaf senescence, thereby keeping a relatively constant number of leaves on the plant at any one time (Ackerly, 1996). This strategy was termed “evergrowing” by Ackerly (1996). Likewise, Frankie et al. (1974) identified three categories of leaf habit in tropical trees in Costa Rica. Those groups include Group I (evergrowing), Group II (leafed out and senesced spo-

radically and maintained green leaves throughout the year), and Group III (deciduous). Osada et al. (2002) noted continual leaf production and senescence in saplings but not in adults of *Elaeagnus argentea* Bl. and indicated that both processes in saplings are related to meteorological factors. Some nontropical deciduous trees can also produce leaves throughout the growing season (Steingraeber, 1982; Burke et al., 1992; Kikuzawa et al., 1996; Seino, 1998, 2001), but leaves of these species senesce as a group at the end of the growing season.

The overlapping of leaf cohorts places *O. acetosella* into a small group of nontropical plant species. Jonasson (1989) reported that both *Dryas octopetala* L. (a trailing shrub of calcareous ridges) and *Cistus monspeliensis* L. (a Mediterranean shrub) can produce leaves throughout the growing season that survive together. *Cistus monspeliensis* stayed evergreen by overlapping continually produced cohorts much like the evergrowing tropical trees but *D. octopetala* produced distinct cohorts of leaves and had periods of maximum and minimum leaf number similar to the pattern observed in *O. acetosella*. Kikuzawa (1984, 1989) indicates that *Euonymus alatus* forma *ciliatodentatus* Hiyama has evergreen and deciduous leaf habits on different portions of the same plant. This strategy, termed “heteroptosis,” appears similar to the pattern of *O. acetosella*, but the evergreen leaves of *E. alatus* survive for two or more years (far longer than those of *O. acetosella* as

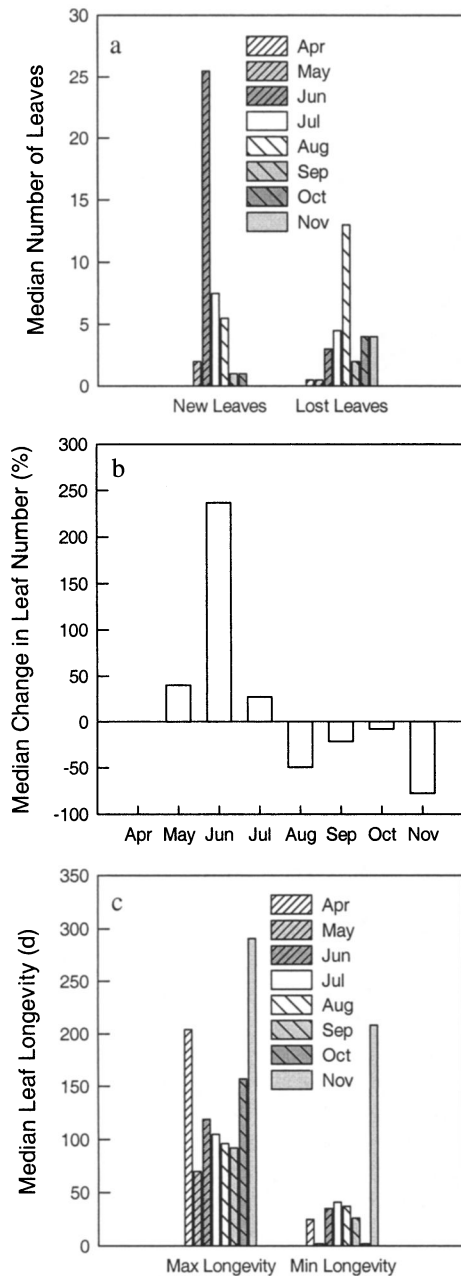


Fig. 3. Patterns of leaf habit in *Oxalis acetosella* in a northern hardwood forest of the Catskill Mountains, New York, USA. (a) Median number of leaves first observed or no longer present. There was a significant difference among months in number of new leaves ($P = 0.0019$) and number of lost leaves ($P = 0.0383$). (b) Median percentage change in population size among months. Differences among months were statistically significant ($P = 0.0003$). (c) Median maximum and minimum leaf longevity among months of first observation of leaves. Maximum leaf longevity differed significantly ($P = 0.0001$) among months but minimum leaf longevity did not ($P = 0.2856$).

described later). Temporally bimodal leaf production also exists in some herbaceous perennial (Jonasson and Widerberg, 1988; Bauer et al., 1991; Uemura, 1994; Zotz et al., 2000) and biennial (Morgan, 1971) plant species, and these different cohorts tend to have different functions. For example, later cohorts tend to survive the winter in evergreen species. The cohorts in *O. acetosella* may have different functions as well (see later).

The average maximum and minimum leaf longevities in *O. acetosella* are closer to the range of leaf longevities reported for deciduous species than evergreen species. Deciduous species have been reported to keep leaves for 39–170 d (Kikuzawa, 1983, 1984; Prock and Körner, 1996; Seiwa, 1999). Evergreen species have been reported to keep their leaves for less than one year up to 30 yr, but mostly more than one year (Kikuzawa, 1984, 1991; Jonasson and Chapin, 1985; Gifford and Foster, 1989; Jonasson, 1989; Clark et al., 1992; Nitta and Ohsawa, 1997; Myers et al., 1998; De Carvalho et al., 1999; Thomas, 2000).

This leaf habit of keeping early season leaves for short periods of time and late season leaves for longer periods may represent another stop on the spectrum of leaf habits in perennial plants (Fig. 4). I suggest that this leaf habit be termed “seasonalgreen” to emphasize the year-round presence of leaves along with an annual maximum and minimum in leaf number. Evergreen species typically keep leaves for more than one year (see earlier), while deciduous species only have leaves during the growing season. The previously recognized wintergreen habit (Uemura, 1994) encompasses species that keep a set of leaves for exactly one year. Evergrowing species (Ackerly, 1996) produce leaves continuously but keep a relatively constant leaf number through the year. *Oxalis acetosella* and *D. octopetala* therefore have leaf longevities and seasonal leaf number patterns similar to deciduous species, yet maintain green leaves throughout the year. This seasonalgreen approach places them between evergrowing and deciduous in the leaf habit spectrum (Fig. 4).

Leaf habit is associated with a series of trade-offs related to leaf function (Reich et al., 1997, 1999; Westoby et al., 2002). Tight relationships exist between leaf longevity and functional traits (Reich, 1993) that are apparently the result of convergent evolution (Ackerly and Reich, 1999). A short leaf life span in a species is linked to high photosynthetic rates (Chabot and Hicks, 1982; Reich et al., 1991, 1992, 1993, 1997, 1999; Reich, 1993; Westoby et al., 2002; Escudero and Mediavilla, 2003), high nitrogen concentrations (Reich, 1993; Reich et al., 1991, 1992, 1997; Westoby et al., 2002; [photosynthetic rates and nitrogen concentrations being highly correlated properties; Field and Mooney, 1986; Reich et al., 1999]), high respiration rates (Reich et al., 1997), thin leaves (Reich et al., 1991, 1992, 1997, 1999; Reich, 1993; Westoby et al., 2002), high relative growth rates (Reich et al., 1992; Ackerly, 1996), high light compensation points (Ackerly, 1996), low carbon concentrations (Ackerly, 1996), high phosphorus concentrations (Reich et al., 1991), and high decomposition rates (Westoby et al., 2002). Collectively, these patterns result in adaptive syndromes of shade-tolerant leaves that conserve resources through long leaf longevity, low respiration rates, low photosynthetic rates, and thick leaves and shade-intolerant leaves that rapidly utilize resources through short leaf longevity, high respiration rates, high photosynthetic rates, and thin leaves (Westoby et al., 2002; Reich et al., 2003). It is unclear, however, how shifts in leaf longevity regulate nutrient use efficiency (carbon gain per unit nutrient) over the life of the leaf (Reich et al., 1992; Westoby et al., 2002; Escudero and Mediavilla, 2003). Senescence of old leaves in trees may also be dictated by shading (Ackerly, 1999) and therefore not tightly linked to leaf traits and changes in leaf physiology wrought by aging (Escudero and Mediavilla, 2003).

The global consistency of relationships among leaf traits is striking (Reich et al., 1997, 1999). The slopes of regression

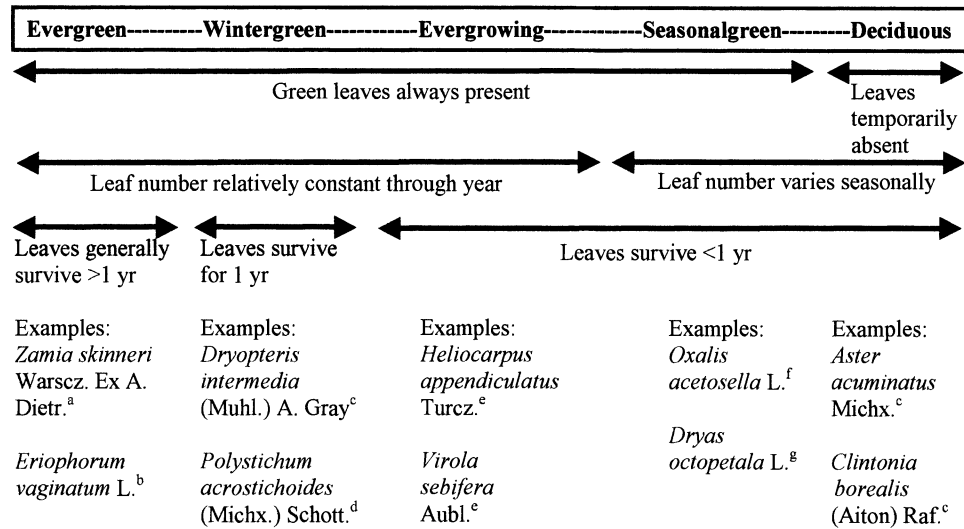


Fig. 4. Classification of leaf habits of perennial plants based on temporal presence of leaves and leaf longevity. References: ^aClark et al. (1992), ^bJonasson and Chapin (1985), ^cMahall and Bormann (1978), ^dMinoletti and Boerner (1993), ^eAckerly (1996), ^fpresent study, ^gJonasson (1989).

lines between the aforementioned variables are consistent across broadly spaced ecosystems, while the y-intercept of those lines varies among sites (Reich et al., 1997, 1999). These global patterns suggest that consistency can be expected within a species across its geographic spread in terms of the functional patterns of its leaves. Differences in traits among leaves of an individual should result in accurate predictions of leaf function based on those traits. The following paragraphs represent a prediction of leaf function within *O. acetosella* based on differences in longevity among its leaves.

Many researchers (Small, 1972; Moore, 1980; Goldberg, 1982; Medina and Francisco, 1994; Escudero and Mediavilla, 2003) have suggested that being evergreen helps a plant to increase its nutrient use efficiency (but see Jonasson, 1989), to promote water retention (Medina and Francisco, 1994; Myers et al., 1997), or to generally tolerate stress (Al-Mufti et al., 1977). *Oxalis acetosella* may be keeping green leaves throughout the year for any of these reasons, but also seems to be specializing leaf function by cohort.

Making use of wintergreen leaves is hypothesized to provide an energy benefit to plants (Chabot and Hicks, 1982; Moore, 1984; Tessier, 2001) by permitting vernal photosynthesis, particularly during warm days (Burkle and Logan, 2003). This leaf habit may also provide a nutrient storage benefit in some species via vernal retranslocation of nutrients from the senescing leaves to the rest of the plant (Moore, 1984).

Deciduous plants control the timing of leaf expansion and senescence to maximize light interception (Gill et al., 1998), eliminate ineffective leaves (Leopold, 1961; Field and Mooney, 1983; Clark et al., 1992), provide for nutrient recovery (Leopold, 1961; Del Arco et al., 1991; Escudero et al., 1992; DeMars and Boerner, 1997), and for general seasonal adaptation (Leopold, 1961).

While leaves are produced throughout the year in *O. acetosella* (Figs. 2, 3a and b) leaves produced later in the growing season tend to have longer life spans than those produced during spring and summer (Fig. 3c). These differences in longevity and survivorship suggest functional differences among cohorts. It appears that *O. acetosella* is producing short-lived leaves with potentially high photosynthetic rates in the spring

to take advantage of high vernal light intensity, moderately long-lived leaves during the summer that must be shade tolerant, and long-lived leaves in the fall that may contain higher levels of structural compounds to survive the winter and provide a photosynthetic benefit to the plant early in spring. Such differences in function among leaf cohorts are known to occur in the biennial *Hydrophyllum appendiculatum* Michx. (Morgan, 1971). Collectively, these cohorts would allow *O. acetosella* to take advantage of the benefits of a range of leaf habits. Future studies should test these predictions.

The exact cause of leaf turnover in *O. acetosella* invites additional questions. While leaves may be produced with certain physiological attributes making them suited to seasonal functions, the continual loss of leaves may be a necessary adaptation that permits continual leaf production. Retranslocation of nutrients with leaf senescence (Leopold, 1961; Del Arco et al., 1991; Escudero et al., 1992) may provide sufficient resources for the continual production of specialized leaves (Jonasson and Chapin, 1985; Chapin et al., 1986). Senescence may, however, not be as planned as the previous hypothesis suggests. Unplanned leaf loss through herbivory, drought, or other disturbance may represent added stress to the plant for which continual leaf production compensates (McNaughton, 1983). Further work should document the cause of leaf loss and relate that loss to leaf function and habit.

In conclusion, *O. acetosella* displays a leaf habit intermediate between evergreen and deciduous. I suggest that this leaf habit be termed “seasonalgreen” to indicate the year-round presence of green leaves on the plant and the annual maximum and minimum in leaf number. The differences in longevity and survivorship among leaf cohorts suggest functional differences among the cohorts. This work provides further details of the leaf phenology of *O. acetosella*. Future studies should examine the ecophysiological implications of this leaf habit (Corlett and LaFrankie, 1998), as well as the possibility that other plant species, which are currently considered to be evergreen or wintergreen, display this seasonalgreen leaf habit.

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