

EDAPHIC DIFERENTIATION IN LASTHENA: A MODEL FOR STUDIES IN EVOLUTIONARY ECOLOGY

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ABSTRACT

The current knowledge of the goldfield genus Lasthena is discussed, emphasizing the possible role of edaphic factors in the divergence of this predominantly Californian genus. Lasthena species occupy a variety of edaphic habitats ranging from serpentine outcrops to salt flats to guano deposits, thriving under specific ion and osmotic conditions that are uninhabitable for the vast majority of species. Studies show that ion accumulation and sequestration are common strategies used to counter osmotic stress, common to most habitats harboring Lasthena species. Inter- and intra-specific variation in tolerance to edaphic conditions has been observed in closely related yet reproductively isolated taxa, suggesting that edaphic factors may have set the stage for the diversification of this genus. Lasthena provides numerous opportunities to examine the link between adaptation, reproductive isolation and speciation.

Key Words: adaptive divergence; California flora; edaphic races; Lasthena; salinity tolerance; serpentine.

According to Lindley and Moore (1876), “they (Lasthena) grow in wet places, and appear to be uninteresting weeds.” They do “grow in wet places,” but studies of Lasthena (Heliantheae: Asteraceae) over the last several decades have shown the genus to consist of anything but “uninteresting weeds.” Commonly known as goldfields, plants of Lasthena occupy large areas of the California landscape, casting spectacular carpets of brightly-colored golden yellow flowers in early spring. A recent molecular phylogenetic study recognized 21 species and subspecies belonging to seven sections (Chan et al. 2001). All but one species are endemic to the Californian Floristic Province. Lasthena kunthii (Less.) Hook & Arn., the only member of the genus found outside western North America, is endemic to vernal pools and wetlands in central Chile (Ornduff 1966). Members of the genus have wide edaphic tolerance and are found in habitats such as coastal bluffs, guano deposits, vernal pools, salt and alkaline flats, serpentine outcrops, deserts, grasslands, and open woodlands (Ornduff 1966, 1993). Members of L. californica sensu Ornduff (Ornduff 1993) have the widest edaphic tolerance within the genus, with populations spanning all but guano habitats. Keck (1959) stated that L. californica sensu Ornduff [then Baeria chrysostoma (Fischer & C. Meyer) E. Greene] was the most abundant composite in California. Other Lasthena taxa have rather restricted distributions, with seven taxa now listed in California Native Plant Society’s “Inventory of Rare and Endangered Plants of California” (CNPS 2001).

Following Ornduff’s extensive monograph (1966), Lasthena has received considerable attention. Early studies examined inter- and intra-specific variation in flavonoid chemistry (Saleh and Bohm 1971; Ornduff et al. 1973, 1974; Bohm et al. 1989; Desrochers and Bohm 1993) to assess biogeographical relationships and determine trends of biochemical evolution in the genus. Electrophoretic work followed to establish evolutionary relationships among closely related taxa within the genus (Crawford and Ornduff 1985; Crawford and Ornduff 1989) as well as within the highly variable L. californica sensu Ornduff (Desrochers and Bohm 1993). More recently, comprehensive phylogenetic studies (Chan et al. 2001, 2002; Desrochers and Dodge 2003) have contributed to our understanding of patterns of divergence in Lasthena. The study by Chan et al. (2001) agrees with observations made earlier (Ornduff 1966, 1976) that divergence patterns in the genus conform to expectations of catastrophic selection and stasis.

Existing knowledge suggests that Lasthena can provide a model system for studies in evolutionary ecology, specifically, in understanding the role of edaphic factors in differentiation. Species of Lasthena have successfully colonized diverse habitats within California, including those that exclude the vast majority of species (Ornduff 1966, 1993; Kingsbury et al. 1976; Vasey 1985; Rajakaruna and Bohm 1999; Noc and Zeder 2000; Parsons and Whelchel 2000). Further, in some sections (e.g., sect. Hologynme [Bartling] A. Gray and sect. Ornduffia R. Chan) all species occupy the same edaphic habitat yet generally do not grow intermixed (Ornduff 1966), while in others (e.g., sect. Pilomeris [Nutt.] Ornduff), species occur contrasting edaphic habitats (Crawford et al. 1985; Vasey 1985). Thus it is plausible to hypothesize that edaphic factors may have played an important role in the diversification of the genus. In this paper, taxa in several sections are discussed with emphasis on the
possible role of edaphic factors in their diversification. Since many endemic species of flowering plants in western North America are edaphic endemics (Krukeberg 1969, 1986), studies of a model genus such as Lasthenia could provide general insights into speciation in a variety of other such edaphically diverse genera.

Lasthenia sect. Amphiachena (DC.) R. Chan: L. californica sensu Ornduff

Lasthenia sect. Amphiachena, formerly known as L. sect. Baeria (Fisch. & Mey.) Ornduff, was recently revised (Chan 2001) to include four species, L. californica DC. ex Lindl. [consists of subsp. californica, subsp. macrantha (A. Gray) R. Chan, and subsp. bakeri (J. T. Howell) R. Chan, L. gracilis (DC.) Greene, L. ornduffii R. Chan, and L. leptalea (A. Gray) Ornduff. Lasthenia californica and L. gracilis were previously recognized as L. californica sensu Ornduff (1993). The two cryptic taxa found within L. californica sensu Ornduff, L. californica subsp. californica and L. gracilis, have been the subject of intense ecological and evolutionary studies (Rajakaruna and Bohm 1999; Chan et al. 2002; Desrochers and Dodge 2003).

A biosystematic study (Desrochers and Bohm 1995) first suggested the existence of two geographical races within L. californica sensu Ornduff based on flavonoid pigments (Bohm et al. 1989; Desrochers and Bohm 1993), allozyme banding patterns, and cypsela characteristics. A detailed ecological study (Rajakaruna and Bohm 1999) suggested that the two races described by Desrochers and Bohm (1995) occur in distinct sets of habitats that can be classified on the basis of ionic stresses and water availability. Race A plants predominate in habitats subject to ionic stress. Although the soils in these environments are ionically harsh, the percent clay content is generally high, increasing the water holding capacity of the soil. Plants are often restricted to moist or even saturated soils in such environments. In contrast, race C plants are found in ionically “benign” inland environments. The soils are often sandy, rocky, and shallow, drying out early in the growing season. The conditions at Jasper Ridge Biological Preserve (Stanford University, San Mateo Co., CA), where the races occur in parapatry, mirror the trends seen across the range of the taxa, with the two races occupying distinct microhabitats: Race A occupying the wet, yet ionically harsh soils at the bottom of the serpentine ridge, while race C occupies the fast-drying, yet ionically less stressful upper reaches (Rajakaruna and Bohm 1999). At Jasper Ridge, race A plants belong to L. californica subsp. californica while race C plants belong to L. gracilis. However, the races do not always correspond to the two taxa recognized by Chan et al. (2001, 2002). A recent study shows that one or both edaphic races have evolved in parallel in both L. californica subsp. californica and L. gracilis, suggesting that racial features may have evolved secondarily in response to edaphic factors (Rajakaruna et al. in press a).

Recent eco-physiological studies (Rajakaruna et al. 2003) indicate that race A plants from both L. californica subsp. californica and L. gracilis are clearly more tolerant of potentially-toxic Na⁺, suggesting that physiological traits responsible for Na⁺ uptake and sequestration may have evolved independently in populations belonging to the two closely related taxa. Schat et al. (1996) provide one of the best examples of parallel genotypic changes in tolerance to an edaphic extreme within a plant species. Their studies have shown that loci conferring copper tolerance have evolved independently in geographically isolated populations of Silene vulgaris Garcke (Caryophyllaceae). In Plantago (Plantaginaceae), the vacuolar Na⁺/H⁺ antiporter activity, thought to confer tolerance to Na⁺ (Apse et al. 1999) is only present in the salt-tolerant P. maritima L. but not in the glycophytic P. media L. (Staal et al. 1991). This difference is thought to be crucial in the ecological divergence of these two species. Sodium is clearly an important element in many of the habitats where race A is found. Whether the presence/absence or level of expression of the Na⁺/H⁺ antiporter gene is responsible for the differences in uptake and accumulation in race A plants is an area worthy of investigation. Ion uptake studies conducted on the two races from Jasper Ridge also indicate that race A is more tolerant of high external Mg²⁺ and low Ca²⁺/Mg²⁺ ratios (Rajakaruna et al. 2003). Both of these traits have adaptive significance in magnesium-rich serpentine and coastal habitats where race A is found. The traits that have been studied (Na⁺, Mg²⁺, Ca²⁺/Mg²⁺) are common features in most habitats where race A is found, thus, it is tempting to hypothesize that differential response to edaphic stresses may have played an important role in the racial divergence of L. californica sensu Ornduff. By extending eco-physiological studies to characterize the physiology of hybrids between the two species (and races), it is possible to appreciate better the role of edaphic factors in diversification.

The findings from ecophysiological studies (Rajakaruna et al. 2003) suggest a correlation between flavonoid differences, edaphic features, and ion accumulation, suggesting a previously unknown adaptive role for flavonoid differences. The primary feature that distinguishes the edaphic races in L. californica subsp. californica and L. gracilis is the flavonoid pigment profile; race C contains sultated compounds, namely sulfated kaempferol and quercitin diglycosides plus prominent eriocitoyl glycosides (Bohm et al. 1974, 1989; Desrochers and Bohm 1993) not found in race C plants. Ecological roles for flavonoid pigments have often been postulated (Bohm 1987), and the case for a correlation with habitat and sulfated flavonoids has been brought forward (Harborne 1975). A large number
of taxa found in habitats with waterlogged and saline conditions contain sulfated flavonoids (Harborne 1975; Barron et al. 1988). In _L. californica_ subsp. _californica_ and _L. gracilis_, sulfated flavonoids occur only in Na⁺-accumulating plants that predominate in ionically-stressed environments. It is possible that sulfation of flavonoids may be beneficial in sulfate-rich environments where race A occurs. Thus, Rajakaruna et al. (2003) hypothesized an edaphically-linked ecological role for the flavonoid differences that first suggested the existence of these two races (Bohn et al. 1974, 1989).

A study on the response to water stress suggests that the two races from Jasper Ridge show different life history strategies in response to water stress (Rajakaruna et al. in press b). Race C plants (_L. gracilis_) adopt a drought avoidance strategy often referred to as phenological escape (Fox 1990; Arenson et al. 1992) and have significantly greater root weight than race A plants under increasing water stress. In contrast, race A plants (_L. californica_ subsp. _californica_) adopt a slow-growing strategy and allocate more biomass to root than shoot. This strategy is commonly seen in herbaceous annuals growing under edaphic stress, specifically under water and nutrient stresses (Kramer 1980; Grime 1994). Since the study was conducted in potting soils, to seek effects of water stress in isolation, it is unclear how the findings relate to conditions experienced in the field. A large-scale experiment using natural soils is required to clarify further the relationship between ion strength, water availability and fitness within environments, and to further explore factors that affect the distribution of these races at Jasper Ridge and across the species’ range. Given our understanding of the environmental variables associated with differences in fitness, it is now possible to conduct detailed analysis of selection gradients (Wade and Kalisz 1990; Dudley 1996) to infer the role of natural selection in achieving fitness differences under field conditions.

Previous studies (Desrochers 1992) suggested low crossability as well as reduced gene flow between races (Desrochers and Bohn 1995) of _L. californica sensu_ Ornduff. A recent study using seven populations of _L. californica_ subsp. _californica_ and _L. gracilis_ show reduced crossability between the two closely related cryptic taxa (Rajakaruna and Whitton unpublished). Examination of intra- and inter-racial seed set as an effect nested within species suggests that the edaphic races are also reproductively isolated. By comparing patterns of seed set with observations of pollen tube growth, it is clear that most of the reduction in seed set is due to post-pollination, prezygotic effects. Interestingly, there is evidence for enhanced prezygotic isolation in the parapatric location at Jasper Ridge. This pattern suggests a possible role for reinforcement in the observed isolation. Flowering times have diverged in the parapatric location with _L. gracilis_ plants always flowering 7–10 days prior to _L. californica_ subsp. _californica_ plants; the pattern is maintained in the greenhouse. Germination tests also revealed evidence for reduced hybrid fitness. Strong ecological selection at the site (Rajakaruna and Bohn 1999) may severely limit introgression. The fate of any hybrids produced is unknown. A transplant study of hybrids in parental habitats would shed light on possible postzygotic mechanisms of isolation. Further studies are needed to clarify the roles of ecological selection versus reinforcement on the patterns of reproductive isolation observed between races and the two cryptic plant taxa.

An understanding of the relationship between traits for adaptation and reproductive isolation is critical to further the hypothesis of edaphic differentiation in _L. californica_ subsp. _californica_ and _L. gracilis_. Studies suggest that reproductive isolation can be achieved as a by-product of a physiological adaptation to unusually soil conditions (Macnair and Gardner 1998). Macnair and colleagues have shown that the linkage block associated with copper tolerance in _Minimus guttatus_ Fischer ex DC. (Scrophulariaceae) also produces hybrid inviability; however, it is unclear if inviability is achieved via pleiotropy or hitchhiking. Nevertheless, their work has clearly documented that natural selection for an adaptive trait (copper tolerance) has caused a gene for postzygotic isolation to spread through the population (Macnair and Christie 1983; Christie and Macnair 1987). Whether such relationships exist between edaphic tolerance and observed reproductive isolation in _L. californica sensu_ Ornduff is worthy of investigation.

_Lasthenia sect. Ptilomeris_ (Nutt.) Ornduff: _L. minor_ and _L. maritima_

_Lasthenia minor_ (DC.) Ornduff occurs in a variety of habitats such as alkali flats, coastal bluffs, sand dunes, pond margins, and disturbed sites while _L. maritima_ (A. Gray) M. Vasey is restricted almost exclusively to islands and offshore rocks harboring seabird nesting and roosting sites (Ornduff 1965, 1966; Vasey 1985). The soils on these sites are high in nitrogen, low in pH, and highly disturbed from the activities of the birds (Vasey 1985). In addition, constant wind and salt spray produce an outright hostile environment.

Ornduff (1966) considered the self-compatible _L. maritima_ to be a recent descendent from the self-incompatible _L. minor_. An electrophoretic study (Crawford et al. 1985) further supported this hypothesis and suggested that speciation probably involved a switch to self-compatibility, development of autogamy, and subsequent divergence driven by edaphic factors. Given that variation for tolerance is first required to colonize the extreme guano habitats, it is likely that self-compatibility arose post-colonization. Whether the switch to self-compatibility arose as a by-product of an adaptation to guano or is directly linked to speciation is not known.

A recent phylogenetic study showed a close relationship between the two species, but it did not conclusively demonstrate that isolation is due to the difference in postzygotic selection between the two species (Harborne et al. 1996). However, Vasey (1985) noted that only truly sympatric sites are occupied by only a few plants appear to show evidence of parapatric populations. Studies on the reproductive ecology of natural interspecific hybrids in the field suggest that it is possible that strong postzygotic selection is responsible for limiting introgression.

The physiological basis of the avoidance in _L. maritima_ is not understood. When vased planted in soils by Vasey (1985) showed a tolerance of guano-modified soils, individuals that extended screening for potential species among populations, which were critical to the discovery of _L. maritima_. Limited studies are critical to the role of _L. maritima_ in the ecological success of the species. The laboratory work has shown that _L. maritima_ accumulates nitrates faster than _L. minor_ (Tischner 2000), and it is possible that the laboratory work has the potential to exist between the two species. Physiological differences between species such as tolerance to excess salt or high osmotic stress, also high nitrate content in the soil, allow _L. maritima_ to grow in these environments. Nitrate uptake has also been shown to affect nitrogen content in the soil (Tischner 2000), and it is possible that the laboratory work will be done to assess the ability of _L. maritima_ to produce an outstanding individual or reduced hybrid for examination.

_Lasthenia sect. Holocarya_, _L. chrysantho, L. globulifera_

All three species in this section have similar habitats and form vigorous, leafy, and fertile hybrid strains. (Ornduff) was suspect in the hybridization of _L. globulifera_, which is also thought to be a direct descendant from the species. _L. chrysantho_ (Green) (Ornduff 1966). The study showed no direct molecular evidence for hybrid origin of _L. ferrisia_.
no or is directly linked to a gene conferring adaptation is not known.

A recent phylogenetic study (Chan et al. 2001) showed a close relationship between the two species, but it did not conclusively support the proposed ancestor-descendant relationship. The close relationship between the two species is reflected by the high fertility of artificial crosses (Ornduff 1966). However, Vasey (1985) reports that at the only truly sympatric site known for the two species, only a few plants appear to be intermediates. Examination of parapatric populations of the two species at three localities failed to reveal any indication of natural interspecific hybridization (Vasey 1985). It is possible that strong ecological selection is responsible for limiting introgression.

The physiological basis for the substrate tolerance in L. maritima is not known. Preliminary studies by Vasey (1985) show that L. minor is not tolerant of guano-modified soils. However, it is possible that extensive screening may reveal tolerant individuals among populations of this species. Such studies are critical to our understanding of the origin of L. maritima. Limited work suggests that L. maritima accumulates nitrates in its foliage (Ornduff 1965), and Vasey (1985) suggests that high nitrate content in the cells may have allowed L. maritima to grow in these osmotically-challenged sites. Nitrate uptake has been well characterized (Tischner 2000), and it is feasible to determine in the laboratory whether physiological differences exist between the two species in this regard. Other physiological differences between the two species, such as tolerance to excess cations such as Na⁺ and high osmotic stress, also common to these sites, have not been examined. Clearly, there is much work to be done to assess mechanisms of tolerance to guano soils and the L. maritima-L. minor complex provides an ideal opportunity to do so. Once trait differences are established between the two species and their adaptive significance determined, it will be possible to examine their genetic basis. Whether traits contributing to adaptation to guano soils also contribute to isolation (i.e., self-compatibility or reduced hybrid fitness) can then be examined.

_Lasthenia_ sect. Hologyme (Bartling) A. Gray; L. chrysanta, L. glabrata, and L. ferrisiae_

All three species in this section occupy saline habitats and form vigorous, moderate to highly fertile artificial hybrids (Ornduff 1966). Hybrid speciation was suspected in the origin of _L. ferrisiae_ Ornduff, putatively from hybridization between _L. glabrata_ Lindl. subsp. coulteri (A. Gray) Ornduff and _L. chrysanta_ (Greene ex A. Gray) Greene (Ornduff 1966). The study by Chan et al. (2001) show minimal molecular variation for species within this section and is uninformative on the possible hybrid origin of _L. ferrisiae_. An interesting observation made by Ornduff (1966) is that these three closely related species, with edaphic requirements that appear to be identical, are never sympatric. A pure population of one of these species may exist within a few meters from a pure population of another. Ornduff (1966) attributes this pattern to occupation of a site on a "first come, first served" basis, yet admits that a detailed ecological study probably would reveal factors that are different among such sites. It is likely that the three taxa differ in their tolerance regime to edaphic features associated with salinity. The species-trio provides yet another setting to explore the relationships among adaptation, reproductive isolation, and diversification.

_Lasthenia_ sect. Ornduffia R. Chan; _L. fremontii, L. conjugens, and L. burkei_

All three species in this section are inter-crossable (Ornduff 1966, 1969). The ranges for _L. conjugens_ Greene and _L. fremontii_ (Torr. ex A. Gray) Greene marginally overlap, however, natural hybrids between the species are very rare (Ornduff 1969). Artificial hybrids between _L. conjugens_ and _L. fremontii_ show remarkable similarity to _L. burkei_ (Greene) Greene, leading Ornduff (1966) to suggest a hybrid origin for this taxon. _Lasthenia burkei_ occurs in vernal pool habitats similar to those occupied by its two relatives, but its geographical range is distinct. Many research tools have been utilized (Saleh et al. 1971; Crawford and Ornduff 1989; Chan et al. 2001) to resolve relationships within this section but have not been able to support conclusively Ornduff's hypothesis for the hybrid origin of _L. burkei_.

Although all three species colonize vernal pools, their distributional pattern within a pool seems to be related to water level, soil moisture, and salinity (Ornduff 1966). Ornduff (1966) claimed a similar situation to that described for the three halophytes in sect. _Hologyme_, where the species are rarely sympatric although they may be occupying sites just a few meters apart. Again, specific edaphic tolerances may exist among these vernal pool taxa and the sites they are restricted to may in fact show micro-scale differences in edaphic features. Only a close examination of these sites, such as our detailed study of the serpentine outcrop at Jasper Ridge (Rajakaruna and Bohm 1999), will reveal patterns of soil heterogeneity in these apparently uniform edaphic habitats. In a study conducted in an artificial vernal pool created at Berkeley, Ornduff (1966) demonstrated that _L. conjugens_ was always restricted to the soil immediately above and below the water level while _L. fremontii_ occurred from water level to the upper limit of soil moisture (Ornduff 1966). _Lasthenia conjugens_ appeared to be the more water-dependent of the two species and may be occupying deeper vernal pools that dry out later in the growing season. Though physiological
differences obviously exist among the three species, the range of tolerance to salinity and osmotic effects is unknown. Characterization of the ecological amplitude of these species and their artificial hybrids may shed light on the importance of edaphic features in the diversification of this group. Other species, especially L. kunthii (Less.) Hook and Arn. and L. glaberrima DC. (L. sect. Lasthenia) are also restricted to vernal pools and wetlands, while L. platycarpa (A. Gray) Greene [L. sect. Platycarpa (H. M. Hall) Ornduff] is found predominately in alkalai flats (Ornduff 1993).

The survey presented here reveals that the majority of Lasthenia species are tolerant of unusual edaphic conditions, and it is reasonable to suggest that these edaphic features have played an important role in the diversification of this relatively small genus. Even within an apparently uniform edaphic habitat, such as a salt flat, populations of different species are rarely sympatric. This strongly suggests that micro-scale differences in edaphic features are likely responsible for their distribution. Although species discussed above are adapted to deal with different specific ionic environments (e.g., heavy metals, magnesium under serpentine, sodium, magnesium under saline, nitrate under guano), an important factor that is common to all these edaphic habitats is the high osmotic pressure of the soil solution. From the information currently available for Lasthenia (Ornduff 1965; Rajakaruna and Bohm 1999; Rajakaruna et al. 2003), it appears that ion accumulation and sequestration is a common strategy used to counter this stress. However, there are inter- and intra-specific differences in mechanisms of tolerance to osmotic stress and these differences may have set the stage for the fascinating ecological diversification seen in the genus.

Many Lasthenia species occur in land that is geologically rather recent, since a large proportion of their present range was covered by sea water during the Miocene and Pliocene (Howard 1951; Axelrod 1956). The inland sea retreated at the close of the Pliocene, although saltwater lakes of varying extent existed in the Central Valley during the Pleistocene (Plint 1947). Some of the lakes and marshes have persisted into the 19th century (Mason 1957) and it is reasonable to speculate that the ancestor of Lasthenia was tolerant of salinity (specific ion effects) and osmotic effects. Salinity and osmotic tolerance may in fact represent ancestral traits that have been retained in the vast majority of species while it has been lost in a few others. Alternately, tolerance to osmotic and salinity effects may have independently evolved in the various species in response to their radiation into unique habitats such as vernal pools, alkalai flats, serpentine outcrops, and guano deposits.

The Hawaiian silversword alliance (Asteraceae: Madinieae) provides perhaps the most spectacular and well-studied example of adaptive radiation in plants (Robichaux et al. 1990; Baldwin 1997). The study by Chan et al. (2001) suggests that salitional diversification has also occurred in Lasthenia, with a rapid initial radiation, perhaps into distinct ecologic niches, followed by long periods of gradual change punctuated by renewed, rapid diversification. Lasthenia has no doubt been immensely successful in adapting to the ecological diversity of its present range similar to other Californian genera where catastrophic selection has supposedly operated (Lewis 1962; Vargas et al. 1999).

Edaphically restricted species provide fascinating examples for the study of plant speciation. The study of the processes leading to the evolution of such species can shed light on the relationship between adaptation and speciation. With the advent of genetic techniques such as the study of quantitative trait loci (QTLs), it is possible to study candidate “speciation genes.” Perhaps the best-known example in this regard is in the genus Mimulus (Bradshaw et al. 1998) where floral traits associated with pollinator preference and reproductive isolation have been characterized. This study implies that genes of large effect can contribute to speciation. A similar association has recently been estabilished in Aquilegia (Ranunculaceae) (Hodges et al. 2002). In both these QTL studies, reproductive isolation is a by-product of adaptation to pollinators, thus providing a direct link between adaptation and speciation.

The genus Lasthenia provides numerous opportunities to examine the link between adaptation to substrate and reproductive isolation. Many closely related species in Lasthenia generally avoid sympathy and appear to be wholly distinct in areas of contact. Thus, these species appear to be both ecologically divergent and reproductively isolated. In Lasthenia, the extent of isolation as well as the extent of ecological differentiation among closely related species, has not been well documented except in the case of L. californica sensu Ornduff (Rajakaruna and Whitten unpublished). Traits that are associated with ecological specialization in closely related species can be identified and their adaptive significance can be demonstrated. If the ecologically divergent species are reproductively isolated, it will be possible to examine any links between adaptation to substrate and reproductive isolation, and thus, identify potential “speciation genes.”

The available phylogenetic information (Desrochers and Bohm 1995; Charn et al. 2001, 2002; Desrochers and Dodge 2003), along with the relatively small size of the genus, low base chromosome number (n = 8), generally annual habit and obligately outcrossing nature, and the ease with which the species can be grown for experimental studies make Lasthenia an ideal model for studies in evolutionary ecology.

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LITERATURE


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Whitton for advice and useful comments on the manuscript.

LITERATURE CITED


LINDLEY, J. and T. MURDER (eds.). 1876. The encyclopaedia, or, the treasury of botany of the vegetable kingdom, with which is incorporated a glossary of botanical terms. Longmans, Green, London, England.


———, and M. GARDNER. 1998. The evolution of edaphic...
Leaf glaucescence is a common trait among plants and it can be easily rubbed off the leaves of Salix (Salicaceae), glaucous species. It is an important characteristic of many species in this large genus and has long been known to some individuals that is characteristic for its ecological role (Gottschalck, 1959).

While attempting to research Salix fragilis L. indoors with light levels similar to those observed that the new leaves acquire any glaucescence. Leaves are normally glaucous in the light. It was uncertain whether the glaucescence is caused by no sun exposure or due to consistent room temperature. Cuttings of this species and other Salix species (Table 1) were placed next to leaves to try to determine if the new leaves were responsive to light or not. The species was selections, 1980, and six sections (Bicknell, 1976).

Cuttings were collected from seven native species (Table 1). From 2002 from Salix fragilis L. These cuttings were from the growth of two full season. These cuttings were placed in individual foam cups on the greenhouse, and grown exposed to the sun for 2 weeks.

**Leaf characteristics**: Salix nigra Makino (Salicaceae) produces a white, powdery glaucous bloom on the underside of the leaves. It is an important characteristic of many species in this large genus and has long been known to some individuals that is characteristic for its ecological role (Gottschalck, 1959).

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