Reproductive ecology of granite outcrop plants from the south-eastern United States

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Abstract

Most of the Piedmont Physiographic Province of the southeastern United States is covered with mixed mesophytic forest of oaks, hickories, and pines. Within this "sea", however, are "islands" of exposed granite and gneiss. A characteristic, and largely endemic, assemblage of plants has adapted to the environmental extremes that bare rock provides by strongly altering their morphology, physiology, and life history. With respect to their reproductive ecology, however, these plants appear very similar to their congeners and to the Piedmont flora as a whole. Except for ant-pollinated *Diamorpha smallii*, most species show the expected range of pollen vectors, including wind, bees, flies, butterflies, moths and one species of hummingbird. Fruit and/or seed dispersal appears to be highly localised and effected primarily by wind and water. If anything, most species appear to possess adaptations against long-distance dispersal, which would carry propagules into the inhospitable matrix of oak-hickory-pine forest. Mating systems are variable, including examples of both self-compatible and self-incompatible taxa. Consistent with the expectation of low gene flow between populations on isolated outcrops, genetic data show strong differentiation and suggest the potential for genetic drift and/or natural selection to result in divergence. Some of the endemic species on granite outcrops have originated by allopolyploidy, whereas others appear to represent products of more gradual divergence in geographical isolation. There is reason to believe that some weedy species of early successful sites were originally restricted to granite outcrops and spread more recently to sites disturbed by human activities.

Introduction and Background

Most of the Piedmont Physiographic Province of the southeastern United States is covered with mixed mesophytic forest of oaks, hickories, and pines. Within this "sea", however, are "islands" of exposed granite and gneiss. Such areas constitute a habitat archipelago, supporting a largely endemic assemblage of plants and animals that are remarkably well-adapted to the environmental extremes that bare rock provides. These outcrops are known locally as "flat rocks" or "cedar rocks" and differ strikingly in vegetation from the surrounding Piedmont forest (McVaugh 1943). They occur from central Alabama to south-central Virginia and range from flat exposures of a few square metres to steeply sloping domes 200 m above base level that cover hundreds of hectares (Quarterman *et al.* 1993).

Originally, biologists speculated that the granite outcrops were of relatively recent origin, their appearance having been initiated through burning by native Americans and hastened by the erosion that accompanied poor lumbering and farming practices of European settlers (*e.g.* Oosting & Anderson 1939). Geological evidence, however, indicates that these rock units are >350 10^6 years old and that the occurrence of exposed rock in the Piedmont probably dates back at least 150 mybp. This molten, igneous rock was intruded into pre-existing country rock and has become exposed in places where the erosional

cycle of the Piedmont has weathered away surrounding rock that proved less resistant (McVaugh 1943). Individual rock outcrops may, therefore, be much younger than might be suggested by the presumption of their existence 150 mybp. The endemic plants and animals have probably "island-hopped" from exposure to exposure as local erosional forces created new outcrops and covered older ones (Wyatt & Fowler 1977).

Weathering of the granite itself produces distinctive patterns and creates special habitats to which plants have adapted (Burbanck & Platt 1964). Uneven weathering of the surface produces rock-rimmed depressions that retain water between sporadic rainstorms in the late winter to early spring. These weathering pits may later become filled with sand and organic debris. Invasion of these depressions by plants speeds the chemical weathering process, as rainwater combines with CO_2 from the plants to produce carbonic acid. On domed outcrops, exfoliation occurs regularly. Huge shells of rock fracture and slide over the top of underlying layers, exposing fresh granite and creating talus at the base of the dome.

Environmental conditions on granite outcrops are harsh and differ sharply from conditions in the adjacent forest. Temperatures on the outcrops typically are much higher than in the forest because of high incident radiation, absorption of heat by the rock, and low evapotranspiration. Temperatures in excess of 50 °C are common at the rock surface during summer months. Moreover, the shallow, mineral soil overlying impervious rock and the low vegetation cover lead to extraordinarily high runoff. It is estimated that >95% of the annual

precipitation in outcrop communities is lost as direct runoff versus only 10%, on average, for the Piedmont of Georgia (Duke & Crossley 1975). These characteristics of granite outcrops, despite their location within a region that receives >1200 mm of annual precipitation, make them islands of desert embedded in a sea of mesic deciduous forest.

The decidedly desertic nature of the outcrops is reflected in the morphological, physiological, and life-history adaptations of the characteristic plants. A number of perennial species tolerate the extremely hot, dry conditions by storing water in succulent stems or leaves (*e.g. Opuntia humifusa, Talinum teretifolium, Portulaca smallii*). Others use CAM (Crassulacean Acid Metabolism), a photosynthetic pathway that enables them to use water very efficiently. By day, their stomata are closed as they store light energy in the form of organic acids. At night, their stomata open to take in CO_2 to be fixed into carbohydrates. Water loss by transpiration through open stomata is therefore minimised in such species as *Diamorpha smallii* and *Sedum pusillum*.

Perhaps the most widespread solution to the desert conditions, however, is drought avoidance. The overall abundance of different life-forms (*sensu* Raunkiaer 1934) shows a much lower proportion of trees and shrubs and a much higher proportion of annual herbs than are found in Piedmont forest (Phillips 1982; Walters & Wyatt 1982). In particular, the winter annual life history is extremely common among the characteristic plants of the granite outcrops. Seeds germinate after late September or early October rains to produce a rosette of frost-resistant leaves. When temperatures start to rise in late March or early April, the plants bolt and flower profusely. By early May, when the shallow soil depressions have become bone-dry, these winter annuals have matured a new crop of seeds, which require an after-ripening period of 4–5 months. Thus, they are able to survive the extremely hot, dry summer months as dormant populations of drought-resistant seeds. In addition to *D. smallii* and *S. pusillum,* there are many winter annuals, some of which, like *Agrostis elliottiana*, are the only annual members of groups that are typically perennial. *Arenaria glabra*, which is sometimes treated as merely a variety of the arctic-alpine perennial *A. groenlandica* (*e.g.* Radford *et al.* 1964), differs chiefly in its annual life history, whose evolution presumably enabled the species to invade granite outcrops.

Predictions

We have, then, a situation on the granite outcrops of the southeastern US that should permit us to make certain predictions about the reproductive ecology of the characteristic plants.

1. The evolution of the characteristic, and largely endemic, outcrop flora will be paralleled by the evolution of the pollinating and dispersing fauna.

2. Because of their importance to colonising ability, self-compatibility and self-pollination will commonly evolve (Baker 1955).

3. As is often seen in island floras, there will be secondary losses of dispersibility and the evolution of dioecy (Carlquist 1974).

4. Population-level genetic differentiation among populations will be strong.

5. Speciation in these small, peripheral isolates will occur rapidly via allopolyploidy or other saltational mechanisms.

6. Because outcrops provide open, relatively low-competition habitats, many weedy species will be able to invade outcrop communities.

Empirical Evidence: Patterns and Processes

Despite the evolution of a number of animals that are endemic to granite outcrops (Quarterman *et al.* 1993), none of these serve as important vectors for pollen or seed dispersal. The activities of most, like the beetle *Collops georgianus* which feeds on pollen and seeds of *Diamorpha smallii* (Shure & Ragsdale 1977; King 1987), are largely destructive. Instead, the characteristic plants are typically pollinated by more wide-ranging, flying insects (*e.g.* Wyatt 1983, 1986). For the most part, the plants appear to have continued to maintain the usual pollination syndromes characteristic of their congeners. The grasses, sedges, and rushes (*e.g. Agrostis elliottiana, Cyperus granitophilus* and *Juncus georgianus*) are wind-pollinated. The aquatic *Amphianthus pusillus* is not water-pollinated, but rather insect-pollinated like its relatives in the Gratioleae of the Scrophulariaceae. *Tradescantia hirsuticaulis* is pollinated primarily by syrphid flies; *Senecio tomentosus*, by butterflies; and *Sedum pusillum*, by small native bees and flies. Few species are bird-pollinated, but this is true of the flora as a whole, probably reflecting the depauperate nectarivorous avian fauna, a single species, the ruby-throated hummingbird (*Archilocus colubris*). Some plant species associated with woods margins near outcrops (*e.g. Bignonia capreolata* and *Aesculus pavia* x *A. sylvatica* hybrids) are regularly visited by this species (dePamphilis & Wyatt 1989). Even when species with highly unusual pollinator relationships occur on the outcrops, they seem merely to have brought these coevolved mutualisms along with them (*e.g. Yucca filamentosa* and the moth *Tegeticula yuccasella*; Pellmyr *et al.* 1996).

The one exception to this generalisation is *Diamorpha smallii*, which has been reported to be effectively pollinated by ants (Wyatt 1981; Wyatt & Stoneburner 1981). The native ants *Formica schaufussi* and *F. subsericea* regularly visit the flowering plants to feed on the small quantities of nectar produced. In doing so, they pick up large numbers of pollen grains on their unusually hairy bodies, presumably transferring them between individuals of this incompatible species. Tests of pollen applied to ant bodies have shown that viability remains high even after several hours (*unpubl. data*), suggesting that these ants do not secrete substances that kill pollen, as many ant species do (Peakall & Beattie 1987).

With respect to vectors for fruit and seed dispersal, the situation is much the same as for pollinators; the characteristic plants show much the same syndromes as their congeners and as the Piedmont flora as a whole. Most species are moved locally by water during convective storms and by wind during occasional wind storms. If anything, however, the species appear to show
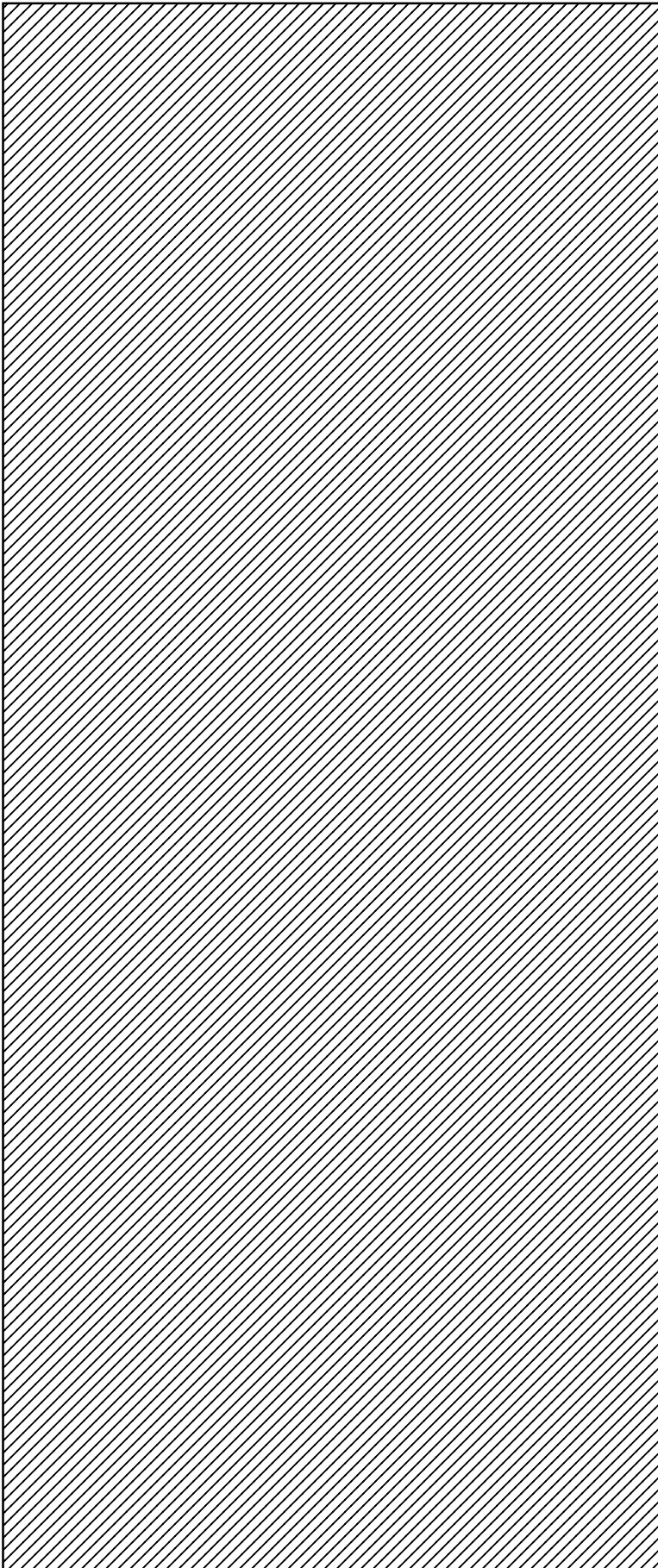
Photographs illustrating some of the characteristic granite outcrop habitats and plants described in the text. **Plate 1**. Stone Mountain, near Atlanta, Georgia, is a 237-hectare granite dome. Such steeply sloping exposures belie the name "flat rocks," which is commonly applied to granite outcrops in the south-eastern United States. **Plate 2**. A small, flat granite outcrop from eastern Alabama. Vegetation mats develop as soil accumulates in depressions weathered in exposed granite. These microcosms represent different stages of succession: *Diamorpha smallii* (Crassulacea), a red-bodied succulent, dominates the shallow pool to the left; fruticose lichens and *Andropogon virginicus* (Gramineae) are abundant in the deeper depression to the right. **Plate 3**. Indicative of the hot, dry environment on granite outcrops is the stem succulent *Opuntia humifusa* (Cactaceae). Here it flowers in mid-May on a granite outcrop in Alabama. **Plate 4**. Vegetation mats over granite develop concentric zones, with earlier colonists displaced to shallower soil at the edges. Here, progressing toward the center, we see *Diamorpha smallii* (Crassulaceae), *Arenaria uniflora* (Caryophyllaceae), *Senecio tomentosus* (Compositae), and *Andropogon virginicus* (Gramineae). **Plate 5**. A large rock-rimmed pool on Heggie's Rock, near Augusta, Georgia, holds water between rainstorms during winter (December-March). This is the type locality for the endangered mat-forming quillwort, *Isoetes tegetiformans*. **Plate 6**. Two other endangered species that grow as aquatics in the rock-rimmed pools are *Amphianthus pusillus* (Scrophulariaceae) and *Isoetes melanospora*. Amphianthus is a monotypic genus that produces long stalks bearing two floating leaves, between which a single, white flower emerges. **Plate 7**. Characteristic of the many winter annuals that occur on granite outcrops, *Sedum pusillum* (Crassulaceae) germinates in fall and over-winters as a frost-resistant rosette. It grows in moss mats of *Hedwigia ciliata*, typically in the shade of *Juniperus virginiana* (Cupressaceae) trees. **Plate 8**. *Tradescantia hirsuticaulis* (Commelinaceae) occurs in the thin woods fringing rock outcrops. Unlike most of the other endemics that have been studied to date, this species has relatively high levels of genetic variation. **Plate 9**. Another winter annual restricted to granite outcrops, *Arenaria uniflora* (Caryophyllaceae) flowers early in the spring. It has been hypothesised that competition for pollinators between the relatively large-flowered, out-crossing plants shown here and another species (*A. glabra*) with even larger flowers has served as the stimulus for the evolution of self-pollination in geographically marginal populations in Alabama and the Carolinas. **Plate 10**. The flowers of *Talinum mengesii* (Portulacaceae) are open for only a few hours early in the afternoon. In addition to strong spatial separation of the anthers and pistil (herkogamy), out-crossing is promoted by a unique pollen germination delay mechanism.

adaptations against too much dispersal. Long-distance transport, for the most part, would likely deliver a propagule to the inhospitable matrix of forest in which the islands of exposed rock occur. An example of this loss of dispersibility, which characterises many island floras (Carlquist 1974), is *Diamorpha smallii*, which differs from its close relatives in the genus *Sedum* by producing fruits that dehisce by a tear-shaped flap at the back of the follicle (Sherwin & Wilbur 1971). This results in the seeds being dropped directly below the parent plant, where they lie dormant during the hot, dry summer.

I suspect that there may occasionally be directed long-distance dispersal of seeds between outcrops. Birds, such as killdeer, often visit the outcrops to drink from the pools and to forage for invertebrates in the seepage areas at the outcrop margins (*pers. observations*). In doing so, they may inadvertently pick up plant progagules in the mud on their feet. After travelling to another outcrop, the propagules may be washed off. It is possible that hawks and vultures, which are also commonly seen in the vicinity of the outcrops drinking from pools, hunting, and riding thermals, act similarly as dispersal vectors. In any event, however, gene flow via these dispersal vectors is likely to be rare. Other species, like the Georgia oak (*Quercus georgiana*), pose additional difficulties, as their seeds are very large. Rarely, they may be transported between outcrops by blue jays, which are known to collect and cache seeds of oaks (Darley-Hill & Johnston 1981).

With the exception of *Isoetes*, plants whose primary mode of dispersal is spores do indeed seem to be moved long distances by the wind. For example, *Pellaea wrightiana* is a common fern of rocky cliffs in the southwestern United States. Some years ago it was collected from a single granite outcrop in North Carolina, more than 1 600 km from the nearest populations in central Texas (Wagner 1965). Similarly, *Astrolepis sinuata*, a fern otherwise restricted to west Texas and northern Mexico, has been collected recently from a small granite outcrop in western Georgia (J R Allison, *pers. comm.*). The fern *Pilularia americana* and a number of lichens and mosses also show long-range disjunctions to outcrops in the southeast (Wyatt & Stoneburner 1982). The species of *Isoetes* that are endemic to granite outcrops in the southeastern United States are a notable exception to the pattern shown by homosporous pteridophytes. Genetic markers suggest that gene flow between outcrop populations of *I. piedmontana, I. melanospora*, and *I. tegetiformans* is very low (Van De Genachte & Wyatt, unpublished). This may be due to the fact that successful colonisation by these heterosporous plants requires simultaneous dispersal not only of the small microspores, but also of the much larger (and presumably, less dispersible) megaspores.

Many of the characteristic granite outcrop species in the southwestern United States are characterised by high rates of outcrossing. Unlike the situation in many island floras (*e.g.* Hawaii; Carlquist 1974), however, there is not a disproportionately high number of dioecious species. The Piedmont flora as a whole is rather depauperate in dioecious species, which constitute only about 3.4% of the flora (Conn *et al.* 1980). The dioecious species that are common on outcrops are mostly woody taxa with wider ranges off the outcrops (*e.g. Juniperus virginiana, Smilax smallii, Forestiera ligustrina*). Dioecy is rare among annuals (Conn *et al.* 1980); thus, it is interesting to note that *Rumex hastatulus* is among the weedy species that may once have been restricted to granite outcrops (see below).

Among the known outcrossers on granite outcrops are taxa demonstrated to be genetically self-incompatible (*e.g. Diamorpha smallii*, Wyatt 1981; *Tradescantia hirsuticaulis, unpubl. data*) and those with well-developed herkogamy (*e.g. Talinum mengesii*, Murdy *et al.* 1970) or dichogamy (*e.g.* central populations of *Arenaria uniflora*, Wyatt 1984). Murdy & Carter (1987) discovered a unique pollen germination delay mechanism in *Talinum mengesii*. They reported that pollen grains deposited on the stigma during the few hours that each flower was open in the early afternoon failed to germinate immediately, but rather were delayed for up to 90 minutes. They speculated that this had the effect of opening up the range of mates siring seeds on each plant and of intensifying gametophytic competition.

Even more numerous, however, are the many taxa, including some in the same genera listed above, that have evolved self-fertilisation. Self-compatibility has been documented in *Sedum pusillum* (Wyatt 1983), which also showed evidence of outbreeding depression, and *Zephyranthes atamasco* (Broyles & Wyatt 1991). *Talinum teretifolium* is self-compatible and highly self-pollinating relative to its diploid progenitor, *T. mengesii* (Murdy 1968; Murdy *et al.* 1970; Murdy & Carter 1985). In this it contrasts sharply with the diploid/allotetrapolid species-pair *Sedum pusillum/Diamorpha smallii*, in which the former is self-compatible and the latter, self-incompatible. The marginal populations of *Arenaria uniflora* studied by Wyatt (1984) are self-compatible and strongly self-pollinating. This also appears to be true for *Phacelia dubia* var. *georgiana* (Levy 1988). I am inclined to discount early reports of a "balanced breeding system" in *Amphianthus pusillus*, in which plants produce immersed cleistogamous flowers at the base of the rosette and emersed chasmogamous flowers in the axils of paired bracts at the tips of elongated, floating branches (*e.g.* Pennell 1935). The "cleistogamous" flowers appear to be merely an earlier developmental stage, observed prior to elongation of the floating branch. True "hydroautogamy" appears to be rare (Philbrick 1991).

Surprisingly few of the species endemic to granite outcrops have been analysed for genetic population structure. Using horizontal starch-gel electrophoresis, Wyatt *et al.* (1992) found low genetic variation in outcrop populations of *Arenaria uniflora*; the percentage of loci polymorphic per population averaged 17.9%; mean number of alleles per locus, 1.0; and expected heterozygosity, 0.048. The selfing populations at the margins of the range were often fixed for alleles that were polymorphic in the central, outcrossing populations. This led to a remarkably high value for G_{ST}, which expresses the proportion of the total gene diversity that exists as differences among populations. The G_{ST} of 0.572 indicates very strong genetic differentiation between outcrops. Similar results were obtained for *Isoetes melanospora* (25.4%, 1.32, and 0.069) and *I. tegetiformans* (12.5%, 1.14, and 0.020) by Van De Genachte & Wyatt (unpublished). Again, strong genetic differentiation was seen for these species (G_{ST} = 0.513 and 0.217, respectively). In contrast, Godt & Hamrick (1993) found high levels of genetic variation in

Tradescantia hirsuticaulis (53.5%, 1.72, 0.157). Nevertheless, the isolated populations were more strongly differentiated than expected (G_{ST} = 0.183). Only in T. *hirsuticaulis* have gene flow estimates > 1 been estimated (Nm = 2.150; Godt & Hamrick 1993). Presumably, there is very little gene flow between outcrop populations of *Arenaria* and *Isoetes*, and genetic drift therefore can have strong effects on these isolated populations.

Recently, Levy *et al.* (1996) have analysed genetic variation in *Phacelia* using restriction fragment length polymorphisms in chloroplast-DNA. They found surprisingly high levels of intraspecific polymorphism, especially in populations of the granite outcrop endemic *Phacelia dubia* var *georgiana*. Levy *et al.* (1996) discounted the likelihood of these polymorphisms being due to gene flow between outcrop populations.

At least two of the most characteristic species endemic to granite outcrops have originated via allopolyploidy. Using isozymes as genetic markers, Murdy & Carter (1985) showed that *Talinum teretifolium* is an allotetrapolid that combines genomes from diploid *T. mengesii* and diploid *T. parviflorum* from the west-central United States and one locality in Alabama (formerly called *T. appalachianum*; Carter & Murdy 1985). Despite conflicting evidence for some loci and a disquietingly high number of "null" alleles, they were able to reject clearly the alternative hypothesis that *T. calycinum* was the second progenitor. Although definitive proof remains elusive, it seems clear that *Diamorpha smallii* also is an allotetrapolid (n = 9), one of whose progenitors is diploid *Sedum pusillum* (n = 4). As Baldwin (1940) suggested, the other progenitor perhaps should be sought among those annual species of *Sedum*, such as *S. nuttallianum* of the west-central United States, with n = 5. Alternatively, *D. smallii* could be related to *Parvisedum*, a small genus of California and northern Mexico with n = 9 (Clausen 1975). Murdy (1968) also suggested that the outcrop endemic *Cyperus granitophilus* may have originated via autopolyploidy from the more widespread *C. aristatus*.

For allopolyploid speciation, hybridisation is a necessary prerequisite. Interestingly, the outcrops seem to represent "hot spots" for hybridisation. To some extent, this may be due to their offering a wide range of habitats, some of which mimic those of other physiographic provinces. For example, the Coastal Plain *Senecio tomentosus* extends its range into the Piedmont on the outcrops, where it comes into contact with *S. anonymus*. Chapman & Jones (1971) documented hybridisation between these species, showing that the F_1 hybrids have reduced pollen fertility. Other species notable for their tendency to hybridise in proximity to granite outcrops include *Quercus* (*Q. georgiana* x *Q. nigra*, *unpubl. data*), *Aesculus* (*A. pavia* x *A. sylvatica*, de Pamphilis & Wyatt 1989, 1990), and *Isoetes* (*I. tegetiformans* x *I. piedmontana*, Van De Genachte & Wyatt unpublished; *I. melanospora* x *I. piedmontana*, Allison 1993).

It would also appear likely that the geographical isolation of populations on granite outcrops could lead to allopatric speciation, especially following a long-distance dispersal event. This process may underlie the origin of the endemics *Phacelia dubia* var *georgiana* and *P. maculata*

(Murdy 1966, 1968; Levy 1991a). Levy's (1991b, 1996) subsequent experimental studies have suggested how reproductive barriers can arise as taxa diverge and strongly hint that new incipient varieties are still being formed. Two other outcrop species that Murdy (1968) advanced as examples of ecogeographical differentiation are *Portulaca smallii* and *Rhynchospora saxicola*. This interpretation, however, may be backwards (see below), as the Coastal Plain habitats occupied by their presumed progenitors are probably younger than the Piedmont outcrops.

Much interest has focused on two of the outcrop endemics that appear to be highly isolated in their families and to have no close relatives; *Amphianthus pusillus* and *Viguiera porteri*. McVaugh (1943) used the former to argue for the great antiquity of the outcrop flora and the latter to show an affinity with the Madro-Tertiary flora of the southwestern deserts, as all other species of *Viguiera* are restricted to that region. More recent evidence from phylogenetic reconstructions based on chloroplast-DNA gene sequences shows that *Amphianthus* is closely allied with the Gratioleae, including *Gratiola*, *Bacopa* and *Mecardonia*, among others (dePamphilis, *unpubl. data*) Similarly, Schilling & Jansen's (1989) data concur with Schilling & Heiser's (1981) suggestion that *V. porteri* is not a *Viguiera* at all, but rather a *Helianthus*.

The weedy species commonly observed on granite outcrops are a very limited subset of the total Piedmont weed flora. The group includes few, if any, exotics (McVaugh 1943). This observation led Wyatt & Fowler (1977) to propose that these species may, indeed, have once been endemics restricted to outcrop habitats. They possessed a number of features, however, that enabled them to invade disturbed habitats, such as old fields, following the arrival of humans. Marks (1983) has advanced this same argument. Thus, for example, rather than understanding the ecotypic adaptation of the old-field dominant grass *Andropogon virginicus* to outcrops, as Chapman & Jones (1975) did, it might be more appropriate to read the evolutionary process in the opposite direction.

Broadening this view a bit, it might be useful to consider the outcrops as the possible original evolutionary springboard for such present-day widespread Coastal Plain plants as *Rumex hastatulus*, *Linaria canadensis*, and *Crotonopsis elliptica*. These pre-eminent weedy plants of the Coastal Plain may have perfected their ability to grow in open, disturbed areas of poor, sandy soil while existing primarily on granite outcrops. When similar habitats became available on the Atlantic and Gulf Coastal Plains, they may have undergone range expansion. Other species that appear to fit this pattern include *Nothoscordum bivalve*, *Schoenolirion croceum*, *Trifolium carolinianum*, *Forestiera ligustrina*, and *Houstonia pusilla*.

References

Allison J R 1993 Technical draft recovery plan for three granite outcrop plant species. Federal Register. US Fish & Woldlife Service, Jackson MI, 1–41.

Baldwin J T 1940 Cytophyletic analysis of certain annual and biennial Crassulaceae. Madroño 5:184–187.

Baker H G 1955 Self compatibility and establishment after long-distance dispersal. Evolution 9:347–349.

Broyles S B & Wyatt R 1991 The breeding system of *Zephyranthes atamasco* (Amaryllidaceae). Bulletin of the Torrey Botanical Club 118:137–140.

Burbanck M P & Platt R B 1964 Granite outcrop communities of the Piedmont Plateau in Georgia. Ecology 45:292–305.

Carlquist S 1974. Island Biology. Columbia University Press, New York.

Carter M E B & Murdy W H 1985 Systematics of *Talinum parviflorum* Nutt. and the origin of *T. teretifolium* Pursh (Portulacaceae). Rhodora 87:121–130.

Chapman G C & Jones S G 1971 Hybridization between *Senecio smallii* and *S. tomentosus* (Compositae) on the granite flatrocks of the southeastern United States. Brittonia 23:209–216

Chapman R H & Jones S B 1975 Ecotypic differentiation in *Andropogon virginicus* (Gramineae). Bulletin of the Torrey Botanical Club 102:166–171.

Clausen R T 1975 *Sedum* of North America North of the Mexican Plateau. Cornell University Press, Ithaca, New York.

Conn J S, Wentworth T R & Blum U 1980 Patterns of dioecism in the flora of the Carolinas. American Midland Naturalist 103:310–315.

Darley-Hill S & Johnston W C 1981 Acorn dispersal by the blue jay (*Cyanocitta cristata*). Oecologia 50:231–232.

dePamphilis C W & Wyatt R 1989 Hybridization and introgression in buckeyes (*Aesculus*: Hippocastanaceae): A review of the evidence and a hypothesis to explain long-distance gene flow. Systematic Botany 14:593–611

dePamphilis C W & Wyatt R 1990 Electrophoretic confirmation of interspecific hybridization in *Aesculus* (Hippocastanaceae) and the genetic structure of a broad hybrid zone. Evolution 44:1295–1317

Duke K M & Crossley D A 1975 Population energetics and ecology of the rock grasshopper, *Trimerotropis saxatilis*. Ecology 56:1106–1107.

Godt M J W & Hamrick J L 1993 Genetic diversity and population structure in *Tradescantia hirsuticaulis* (Commelinaceae). American Journal of Botany 80:959–966.

King P S 1987 Macrogeographic and microgeographic structure of a spatially subdivided beetle species in nature. Evolution 41:401–416

Levy F 1988 Effects of pollen source and time of pollination on seed production and seed weight in *Phacelia dubia* and *P. maculata* (Hydrophyllaceae). American Midland Naturalist 119:193–198.

Levy F 1991a Morphological differentiation in *Phacelia dubia* and *P. maculata*. Rhodora 93:11–25.

Levy F 1991b A genetic analysis of reproductive barriers in *Phacelia dubia*. Heredity 67:331–345.

Levy F, Antonovics J, Boynton J E & Gillham N W 1996 A population genetic analysis of chloroplast DNA in *Phacelia*. Heredity 76:143–155.

Marks P L 1983 On the origin of the field plants of the northeastern United States. American Naturalist 122:210–228.

McVaugh R 1943 The vegetation of the granitic flatrocks of the southeastern United States. Ecological Monographs 13:119–166.

Murdy W H & Carter M E B 1985 Electrophoretic study of the allopolyploidal origin of *Talinum teretifolium* and the specific status of *T. appalachianum* (Portulacaceae). American Journal of Botany 72:1590–1597.

Murdy W H & M E B Carter 1987 Regulation of the timing of pollen germination by the pistil in *Talinum mengesii* (Portulacaceae). American Journal of Botany 74:1888–1892.

Murdy W H 1966 The systematics of *Phacelia maculata* and *P. dubia* var. *georgiana*, both endemic to granite outcrop communities. American Journal of Botany 53:1028–1036.

Murdy W H 1968 Plant speciation associated with granite outcrop communities of the southeastern Piedmont. Rhodora 70:394–407.

Murdy W H, Johnson T M & Wright V K 1970 Competitive replacement of *Talinum mengesii* by *T. teretifolium* in granite outcrop communities of Georgia. Botanical Gazette 131:186–192.

Oosting H J & Anderson L E 1939 Plant succession on granite rock in eastern North Carolina. Botanical Gazette 100:750–768.

Peakall R & Beattie A J 1987 Pseudocopulation of an orchid by male ants: A test of two hypotheses accounting for the rarity of ant pollination. Oecologia 73:522–524.

Pellmyr O, Leebens-Mack J & Huth C J 1996 Non-mutualistic yucca moths and their evolutionary consequences. Nature 380–155:156.

Pennell F W 1935 The Scrophulariaceae of eastern temperate North America. Philadelphia Academy of Natural Sciences Monographs 1:1–650.

Philbrick CT 1991 Hydrophily: Phylogenetic and evolutionary considerations. Rhodora 93:36–50.

Phillips D L 1982 Life forms of granite outcrop plants. American Midland Naturalist 107:206–208.

Quarterman E, Burbanck M P & Shure D J 1993 Rock outcrop communities: Limestone, sandstone and granite. In: Biodiversity of the southeastern United States/Upland terrestrial communities (eds W H Martin, S G Boyle & A C Echternacht). John Wiley & Sons, New York, 35–86.

Radford A E, Ahles H E & Bell C R 1964 Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill, North Carolina.

Raunkiaer C 1934 The Life-forms of Plants and Statistical Plant Geography. Oxford University Press, London.

Schilling E E & Heiser C B 1981 An infrageneric classification of *Helianthus* (Compositae). Taxon 30:393–403.

Schilling E E & Jansen R K 1989 Restriction fragment analysis of chloroplast DNA and the systematics of *Viguiera* and related genera (Asteraceae: Heliantheae). American Journal of Botany 76:1769:1778.

Sherwin PA & Wilbur R L 1971 The contributions of floral anatomy to the generic placement of *Diamorpha smallii* and *Sedum pusillum*. Journal of the Elisha Mitchell Scientific Society 87:103–114.

Shure D J & Ragsdale H L 1977 Patterns of primary succession on granite outcrop surfaces. Ecology 58:993–1006.

Wagner W H 1965 *Pellaea wrightiana* in North Carolina and the question of its origin. Journal of the Elisha Mitchell Scientific Society 81:95–103.

Walters T W & Wyatt R 1982 The vascular flora of granite outcrops in the Central Mineral Region of Texas. Bulletin of the Torrey Botanical Club 109:344–364.

Wyatt R & Fowler N L 1977 The vascular flora and vegetation of the North Carolina granite outcrops. Bulletin of the Torrey Botanical Club 104:245–253.

Wyatt R & Stoneburner A 1981 Patterns of ant-mediated pollen dispersal in *Diamorpha smallii* (Crassulaceae). Systematic Botany 6:1–7.

Wyatt R & Stoneburner A 1982 Range extensions for some cryptogams from granite outcrops in Alabama. Bryologist 85:405–409.

Wyatt R 1981 Ant-pollination of the granite outcrop endemic *Diamorpha smallii* (Crassulaceae). American Journal of Botany 68:1212–1217.

Wyatt R 1983 Reproductive biology of the granite outcrop endemic *Sedum pusillum* (Crassulaceae). Systematic Botany 8:24–28.

Wyatt R 1984 The evolution of self-pollination in granite outcrop species of *Arenaria* (Caryophyllaceae) I Morphological correlates. Evolution 38:804–816.

Wyatt R 1986 Ecology and evolution of self-pollination in *Arenaria uniflora* (Caryophyllaceae). Journal of Ecology 74:403–418.

Wyatt R, Evans E A & Sorenson J D 1992 The evolution of self-pollination in granite outcrop species of *Arenaria* (Caryophyllaceae) VI Electrophoretically detectable genetic variation. Systematic Botany 17:201–209.