GREEN BLACKTOP PETER DEL TREDICI

Peter Del Tredici is a Lecturer in the Department of Landscape Architecture at Harvard Graduate School of Design. He teaches courses on urban ecology, soils, and sustainable landscapes. He is a botanist and senior research scientist at the Arnold Arboretum of Harvard University.

The plants that flourish on derelict urban wasteland are famous (or infamous) for their ability to grow under extremely harsh conditions. Through a quirk of evolutionary fate, many of them have evolved life-history traits in their native habitats that have "preadapted" them to flourish in cities. Indeed, several studies have shown that many common urban plants are native either to limestone cliff habitats and rocky outcrops or dry, open grasslands with neutral or alkaline soils (Gilbert 1989; Wittig 2004; Larson et al. 2004; Lundholm and Marlin 2006). The authors argue—by analogy—that cities with their tall, granite-faced buildings and concrete foundations are biologically equivalent to the natural limestone cliffs where these species originated. Similarly, they suggest that the increased use of de-icing salts along walkways and highways has resulted in the development of high pH microhabitats that are often colonized by either grassland species adapted to limestone soils or salt-loving plants from coastal habitats.

The concept of preadaptation is defined as "an anatomical or physiological trait which evolved under one set of ecological conditions and, by chance, proves advantageous under a completely different set of circumstances" (Del Tredici 2010). It is a powerful idea for understanding the emergent ecology of cities because it helps answer questions about why some species are common in urban habitats and others not. In general, plants that can survive and reproduce under urban conditions without human assistance need to be *flexible* (i.e. non-specialized) in all aspects of their life-history, from germination through seed production and dispersal. They also need to be *opportunistic* in their ability to take advantage of locally abundant resources (mainly water and nutrients) that may be available for only a brief period of time. And finally, they need to be tolerant of the stressful growing conditions caused by an abundance of pavement and a paucity of soil (Baker 1974; Del Tredici 2010).

In nature, these types of plants tend to come from habitats that naturally experience high levels of disturbance and/or environmental stress, such as seasonal flooding (river and stream banks), burning or grazing (natural grasslands and prairies), sun and wind exposure (cliffs and rock outcrops), soil disturbance (eroded slopes), and high soil salt concentrations (coastal and desert areas) (Salisbury 1961; Wittig 2004). Interestingly, a number of species that are commonly found in cities, mainly annuals of European origin, seem to have no known natural habitats. Many of these so-called anecophytes have arisen through the process of hybridization and show specialized adaptations to habitats associated with agriculture, urbanization, and/or industrialization (Salisbury 1961; Meerts et al. 1998; Wittig 2004).

THE NATURE OF URBANIZATION

One of the primary distinguishing features of the urban environment is the ubiquitous presence of physical disturbance associated with the construction

Purslane (*Portulaca oleracea*) growing in a "trifecta" of granite, blacktop and concrete.

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and/or maintenance of its infrastructure. At any given point in time, a significant portion of the urban fabric of economically vibrant cities is in the process of being torn up and rebuilt. This situation leads to the development of a constantly shifting mosaic of opportunistic plant associations dominated by disturbance-adapted, early successional plants, technically known as *ruderals* (Gilbert 1989; Kowarik 1995; Chocholoušková and Pyšek 2003; Kowarik 2005). In economically depressed cities of the United States—such as Detroit, Michigan, or Gary, Indiana—that are experiencing shrinkage rather than growth, a large percentage of the urban core has been abandoned for significant periods of time, upwards of forty years. In such cases succession is allowed to proceed without interference from people, and the vegetation comes much closer to reaching "maturity" than it does in more prosperous cities where ongoing maintenance and economic development promote a more rapid turnover in spontaneous plant associations (Muratet et al. 2007; Rink 2009).

A second distinguishing characteristic of urban areas is the abundance of concrete buildings and asphalt paving. Because such structures absorb and retain head—to say nothing of the cars, air conditioners, heating units, and electrical equipment that generate heat—the annual mean temperatures of large urban areas (i.e., with populations in excess of a million people) can be up to 3° C (5.4° F) warmer than the surrounding nonurban areas; on extreme occasions the temperature differences between the city and the countryside can be as high as 12° C (21.6° F) (Sieghardt et al. 2005). The abundance of buildings and impervious pavement in cities can also have a profound effect on hydrology by decreasing water infiltration, increasing runoff, and compacting the soil, all of which tend to reduce water availability and create stressful drought conditions for plants (Arnold and Gibbons 1996; Paul and Meyer 2001).

While increased temperature is probably the most ecologically significant factor that distinguishes the city from the surrounding countryside (Ziska et al. 2004; George et al. 2007), several other climatological features associated with urbanization can have profound impacts—often significantly positive—on the growth of plants, including elevated levels of carbon dioxide, altered solar radiation regimens, altered wind patterns, decreased humidity, increased or decreased ozone levels, increased soil temperatures, and extended growing season length (Gregg et al. 2003; Sukopp 2004; George et al. 2009).

A third distinguishing feature of the urban environment is its high concentration of non-native plants relative to the surrounding countryside (Kowarik 1995). Some of these plants have escaped from cultivation for agricultural or ornamental purposes; some are unintentionally introduced, disturbance-adapted "weeds"; and some are native to the area. Together they form cosmopolitan vegetation associations that dominate abandoned, degraded, or neglected urban land and mimic the diversity of the human population of the cities in which they grow (Del Tredici 2010).

When one couples the ecosystem impacts of well-adapted, spontaneous vegetation with the ubiquitous disturbance and environmental stress that is characteristic of cities, one has all the components necessary to describe a cyclical succession pattern that is constantly being interrupted by human activity and dominated by so-called pioneer species. With apologies to J. P. Grime (1977), the simplistic model presented in Figure 1 is a reinterpretation of his three basic plant strategies—the ruderal, the competitive, and the stress-tolerant—as drivers of succession in urban environments.

Fall Panicum *(Panicum dichotomiflorum)*
Tree of Heaven (*Ailanthus altissima*)
Prostrate knotweed (Polygonum aviculare)
Spotted spurge (Chamaesyce maculata)

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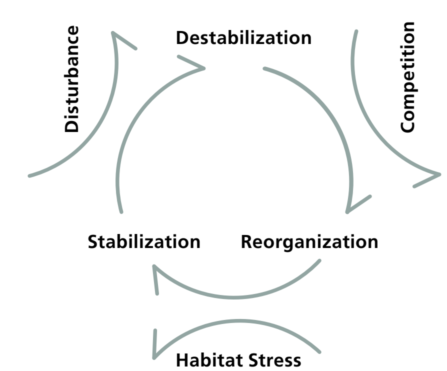
Fig. 1



Tufted Lovegrass *(Eragrostis pectinacea)*
Carpetweed *(Mollugo verticillata)*
Smooth Crabgrass *(Digitaria ischaemum)*
An Urban Krakatoa
Road salt collects in street cracks

Meerts, P., T. Baya, and C. Lefèbvre. 1998. Allozyme variation in the annual weed species complex, *Polygonum aviculare (Polygonaceae)* in relation to ploidy level and colonizing ability. *Plant Systematics and Evolution* 211: 239–256.

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THE URBANIZATION OF NATURE

One of the most ubiquitous and distinctive niches in the urban environment, and the focus of the remainder of this article, is the familiar sidewalk or roadway crack that develops when paving wears out the interface zone where one type of paving material is laid next to another, most often concrete and blacktop, but also including granite and brick. Because these paving materials have different densities and porosities, they respond differently to changes in temperature, pressure, and moisture (Wessolek 2008). This causes them to separate from one another when stressed by the weight of traffic or the formation of ice, thereby creating a relatively resource-rich microhabitat where soil and water (along with road salt and petroleum products) collect and plants can get established.

Observation has shown that many such interstitial "crack plants" share a number of life-history traits, including: 1) an annual life cycle; 2) seeds that germinate with warm temperatures in late spring or early summer; 3) a preference for or tolerance of neutral or alkaline soils; 4) a high level of drought tolerance; 5) a prostrate or mat-forming growth habit that is resistant to being stepped on by people or driven over by vehicles; and 6) a single dominant tap-root (as opposed to producing adventitious roots along their stems) that allows it to fully exploit a minimal defect in an vast impervious surface (Salisbury 1961; Gilbert 1989; Del Tredici 2010).

In a striking example of what might be called *convergent preadaptation*, five of the most common crack species found in cities of northeastern North America—carpetweed (*Mollugo verticillata*) from Central America, purslane (*Portulaca oleracea*) of unknown origin (India, perhaps), spotted spurge (*Chamaesyce maculata*) from eastern North America, and prostrate knotweed (*Polygonum aviculare*) and smooth crabgrass (*Digitaria ischaemum*) from Europe—display remarkably similar morphologies despite their far-flung geographical origins and diverse botanical backgrounds. By exploiting the seams in the urban fabric, this quintet of prostrate, summer annuals demonstrates how natural selection, working through the mechanism of preadaptation, can adjust to the unnatural selection pressures of the city.