Hacquetia
DOI: 10.2478/hacq-2020-0016
sciendo

Plant species occupy different habitats on the fortress walls in Elbasan, Albania

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Key words: colonization, urban ecology, wall flora.

Ključne besede: poselitev, urbana ekologija, zidna flora.

Abstract

Vegetated walls are an important habitat for urban biodiversity. We conducted an analysis of the plant species that grow on the Elbasan, Albania fortress walls. Walls vary in age from 4th to 21st century, and in composition. On 71 walls we assessed 2787 plants of 35 species and recorded plant size, presence of flowers or fruits, height from the ground, crevice depth, wall aspect, wall age and composition, and distance to nearest opposing wall. Eleven species, two of which were ferns, composed 93.8% of the plants. The vast majority of plants flowered and fruited on the walls. Plant density ranged from 0.1–70 plants/m^2. Species distributions varied significantly based on height on the wall, crevice depth, aspect and distance to the opposing wall. These differences may be influenced by dispersal mechanisms, moisture, substrate composition, and other important environmental factors. For example, *Antirrhinum majus* was generally found high on south facing walls in deep cracks whereas *Umbilicus rupestris* was found lower on north facing walls in shallower cracks. It is important that older walls colonized by plants be maintained such that a native flora can persist where natural rocky features are lacking.

Izvleček

Z vegetacijo obrasli zidovi so pomemben habitat za biodiverzitetourbanega okolja, zato smo naredili analizo rastlinskih vrst, ki uspevajo na zidovih trdnjave v Elbasanu v Albaniji. Starost zidov je od 4. do 21. Stoletja, razlikujejo pa se tudi po sestavi. Na 71 zidovih smo zabeležili 2787 osebkov, ki pripadajo 35 rastlinskim vrstam in izmerili njihovo velikost, prisotnost cvetov ali plodov, višino rastišča od tal, globino vrzeli med zidaki, ekspozicijo zidu, njegovo starost in oddaljenost od najbljižjega nasprotnega zidu. 93,8% vseh osebkov pripada enajstim rastlinskim vrstam, dve izmed njih sta praproti.. Večina rastlin na zidovih je cvetela in plodila. Gostota rastlin je bila med 0,1–70 na m^2. Razširjenost vrst se je značilno razlikovala glede na višino zidu, globino vrzeli, ekspozicijo in oddaljenostjo od nasprotnega zidu. Razlike so lahko posledica mehanizmov razširjanja, vlažnosti, sestave substrata ali drugih pomembnih rastiščnih dejavnikov. Vrsto *Antirrhinum majus* smo na primer običajno najšli visoko na južnih zidovih z globokimi vrzelmi, medtem ko *Umbilicus rupestris* uspeva nizko na severnih zidovih s plitkimi razpokami. Kjer ni prisotnih naravnih skalnatih habitatov, je pomembnoohranjati starejše zidove, porasle z rastlinami, saj tako lahko omogočimo uspevanje domorodnih vrst.

Received: 16. 4. 2020
Revision received: 17. 7. 2020
Accepted: 21. 7. 2020

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Introduction

Ever since humans started building walls they have been colonized by plants. Walls provide habitat for vegetation, which then creates resources and habitat for pollinators and other wildlife species (Jim 1998, Ricotta et al. 2001, Gaston 2010, Lososová & Láníková 2010, Baldock et al. 2015). Thus, vegetated walls are an important component of urban biodiversity (Kuhn et al. 2004, Celesti-Grapow et al. 2006, Brandes 2010). For example, Madrea et al. (2015) determined that vegetated facades, which are walls created for vegetation, are important habitat for spiders and beetles. A number of studies have investigated the ecology of these "man-made cliffs" and the popularity of ideas such as "vertical greening" in urban environments have caused a recent increase in interest (Lundholm and Richardson 2010, Francis 2011).

Urbanization can be considered a process that changes flora through a series of filters such as habitat availability, spatial arrangement, species pool and the unique evolutionary selection pressures on populations persisting in urbanized areas (Williams et al. 2009). Urbanization changes community composition through novel combinations of available species (Angold et al. 2006), and often shifts communities from more specialized to more generalist species (McIntyre et al. 2001, Geslin et al. 2013).

Walls are habitats with a highly heterogeneous flora composed partly or primarily of native species assembled from different habitats, e.g. rocky surfaces and ruderal habitats (Wittig 2002), and partly of non-native species (Woodell & Rossiter 1959, Holland 1972, Lisci & Pacini 1993, Simonová 2008, Láníková & Lososová 2009). This is why high floristic diversity is found in many wall habitats (Kolbek 1997, Láníková & Lososová 2009). A number of studies have assessed the plant communities that grow on walls (e.g. Brullo & Guarino 1998, Swierkosz 2004, 2012, Kolbek 1997, Kolbek et al. 2015, Jasprica et al. 2020). Wall phytosociological relevés tend to be heterogeneous with a large number of species and high species overlap (Duchoslav 2002, Kolbek et al. 2015).

Walls are harsh substrates for plant colonization and establishment. The vertical face of a wall is generally difficult to colonize with few niches for propagules to lodge. Seeds may by chance land in small crevices but larger crevices facilitate establishment. The chance of germination and establishment depends on the size, location and substrate of the crevice (Lisci & Pacini 1993). Soil deposition is often minimal or non-existent and insufficient moisture and nutrients severely limit germination. Depending upon the topography of the microsite, the young plant may have to obtain sufficient resources to send out roots to grip the surface. In addition, the geotropic responses of shoots and roots may be distorted by habitat verticality. Because walls are a vertical surface drought may be constant with rainfall infrequently falling inside the crevices; however, in some cases water flowing down the wall surfaces may provide sufficient moisture. On exposed walls, direct solar radiation heats up the stones, which have higher thermal capacity than soil and daytime heat accumulation can reach harmful levels. The heat loading could also dry up soil in the crevices. Alternatively, walls along narrow roads and on northerly exposures may be shaded enough to reduce moisture loss but this also reduces photosynthetic rates. Wall chemistry may be restrictive to plant life as well. The calcareous mortar between stones and bricks is usually strongly alkaline (Bates et al. 1956, Darlington 1981). Urban areas favor plants adapted to base-rich soils (Chocholouskova & Pysek 2003, Godefroid & Koedam 2007, Thompson & McCarthy 2008) and the local pool of these species can be important in their spread to wall habitats.

Differing wall characteristics may influence the species found on the walls (Lisci & Pacini 1993, Jim 1998, Jim & Chen 2010, Yalcinalp & Meral 2017) with wall material, stone dimensions, surface smoothness, surface moisture, weathering status, crack condition, wall aspect, inclination and exposure influencing the species found. Many of the walls in these studies are backed by soil, i.e., retaining walls, and would have different ecological characteristics than walls that are the sides of buildings or are freestanding due to the potential access to soil, nutrients and moisture on the other side of the wall (Lisci & Pacini 1993, Lososová & Láníková 2010).

Studies in central Italy found that most wall species were anemochorous. The seeds of the two species most typical of these walls, *Parietaria judaica* and *Sonchus tenerrimus*, are blown in large quantities against the walls and succeed in germinating and taking root (Lisci & Pacini 1993). However, in a study of vegetated Czech walls, myrmecochory was found to be important after observations that seeds of many of the plant species growing near walls were carried directly into wall crevices by ants (Lososová & Láníková 2010). In Czech Republic, traits positively associated with the ability of species to colonize wall habitats include the presence of summer green leaves, annual life span, CR life strategy (Grime 2001), and reproduction mostly by seeds that are dispersed by ants. These species are also characterized by their high demand for nutrients, warmer temperatures, alkaline substrates and light (Lososová & Láníková 2010). The high nutrient demand of the plant species is not surprising, considering the enrichment of wall habitats by nutrients from the surrounding urbanized environments (nutrient-rich dust, nitrogen and phosphorus in water and soil, and the activities of animals). There is also strong evidence of vegetative propagation for some species. For example, Lisci & Pacini (1993) found that species spread across walls by stolons and rhizomes.

Brandes (2010) found >100 species growing on old walls in Berat and Gjirokastër, Albania. The species were primarily native forbs but also included non-native forbs and woody plants. Wall flora is endangered outside historical settlements because of the use of concrete construction for the vast majority of new walls. As in this study and on walls in other countries of southern Europe, *Parietaria judaica* is the most common species.

Walls differ from cliffs in many ways but are similar in that the opportunities for a propagule to find purchase in a beneficial microsite are limited. In Czech Republic, cliffs are more stressful and lower in nutrients than walls. Cliff environments select for oligotrophic species compared to the higher nutrient wall environments. Cliffs are colonized by CSR and C life strategists and more wind dispersed species compared to the more ruderal and competitive wall habitats (Láníková & Lososová 2009, Lososová & Láníková 2010).

The hypothesis posed in this study examines the distribution of plants on the fortress walls in Elbasan, Albania. Ha: Plant distributions are non-random in respect to measured environmental variables. Ho: Plant species are distributed randomly.

Methods

The interior and exterior walls of the Elbasan fortress (134 m elevation, 34T 422845 Easting 4551845 Northing) were sampled from February–May 2019. This is the largest fortress in Albania occupying an area of 10.2 ha. The first fortress on the site was during the Illyrian period (4th century BC), however, little remains of these walls. When the region was incorporated into the Roman Empire, one of the most important Roman Roads, the Via Egnatia, was built through Elbasan and it connected Constantinople to Rome. To guard the Via Egnatia, the Romans built a fortress on the site which was later largely destroyed. The Roman Emperor Justinian rebuilt the walls in the 4th and 5th centuries and remnants of these walls are still present. The fortress later became part of the Byzantine Empire and bricks from this period are evident in many places. Elbasan became part of the Ottoman Empire in 1446. The 17th century was the prime period for the fortress with 2000 houses and 900 shops located inside the outer fortress walls. Today many outer and inner walls of mixed Byzantine and Ottoman construction still remain, however, many walls have been destroyed or repaired such that the original outer wall is not visible. The remains of the Via Egnatia runs through the middle of the Fortress.

Initially, all of the vegetated walls of the fortress were investigated and characteristics including the location, aspect, and general description of the wall materials and amount of vegetation on a scale of 1–5 scale were recorded (1 = one or a few small plants, 2 = 1–5% cover, 3 = 5–20% cover, 4 = 20–50% cover , 5 = >50% cover). A study unit was defined as a section of wall with a uniform composition; that is, if the wall material or age changed significantly, a separate study unit was assigned. All walls were vertical without horizontal surfaces except in cracks. The flat tops of walls were not examined in this study. Plants rooted at the junction between the wall and the ground surface were not included in the study.

Wall vegetation was sampled, using the variables listed below, with 9 m^2 plots on 52 walls and with 3 m^2 plots on 19 walls which had extremely dense vegetation. Twenty-two walls were sampled on the outside of the fortress and 49 on the inside. Walls were sampled to a height of 3 m because that was the highest that could be accurately sampled. A few of the walls were less than 3 m tall. A total of 482 m^2 of wall was sampled for plants. Plot locations were chosen subjectively in order to ensure that walls in all parts of the fortress with various aspects, levels of plant density, and composition were sampled as equitably as possible. Species were identified using the following: Flora of Albania (Paparisto et al. 1988, Qosja et al. 1992, 1996, Vangjeli et al. 2000), Flora Europaea (Tutin et al. 1964, 1968, 1972, 1976, 1980), Illustrated Flora of Albania (Pils 2016). Species nomenclature followed The Plant List (2013) and Euro+Med Plant Base (2019). Plant specimens were deposited in the Aleksander Xhuvani University herbarium.

Plot data that was recorded includes the following:

- Aspect – north = 1, east = 2, west = 3, and south = 4. The numbering system takes into account the level of exposure with south facing walls having the greatest sun exposure and north facing walls the least (Sternberg & Shoshany 2001).
- Distance to opposing wall. Walls on the outside of the fortress were given a value of 50 m to the opposing wall. If the opposing wall is near the wall environment will be shadier as opposed to when the opposing wall is far.
- Height & width of wall.
- Relative age (1= new wall, 5 = very old wall (an old wall has little evidence of recent construction or repair).

- Overall mean crevice depth for the wall (1 = smooth with just a few crevices, 5 = many very deep crevices in the wall). Because this is a generalization for a plot, a smooth wall may, for example, contain a few deep crevices.
- Composition – stone, mortar, wood, brick, stucco and cement. 0 = the material is not in the wall, 1 = a small amount of this material in the portion of the wall comprising the plot, 5 = plot is completely composed of this material. The amount of the wall that had been whitewashed was also recorded on the same 0 to 5 scale.

For each plant in the plot the following was measured:

- Species (identified using Paparisto et al. (1988), Qosja et al. (1992, 1996), Vangjeli et al. (2000), Tutin et al. (1964, 1968, 1972, 1976, 1980), Pils (2016).
- Approximate plant size (length of the plant times width).
- Presence of flowers or fruit.
- Distance of the plant from the ground surface.
- Crevice depth.

MANOVA, based on Pillai's trace, was conducted on the height, crevice depth, aspect and distance to opposing wall data for the 11 most common species (those with >30 individuals) followed by a Games-Howell post-hoc test (SPSS 2017). Although the data was non-normal and heteroscedastic the MANOVA is considered robust enough for these deviations from normality.

Environment-species and environment-plot relationships were explored by Canonical Correspondence Analysis (CCA), a constrained ordination method (ter Braak & Smilauer 2002, McCune & Mefford 2006), using PC-ORD (Wild Blueberry Media LLC 2018). In general, the longer the environmental vector, the stronger the relationship of that variable with the community. The position of a species relative to an environmental vector can be used to interpret the relationship between various species and the measured environmental variables. In the biplot, axis 1 represents the direction of the greatest amount of variation, and axis 2 represents the 2nd-greatest amount of variation in the data set. The 11 most common species were ordinated with Canonical Correspondence Analysis (CCA) with the plot level characteristics enumerated above and the number of individuals of each species in a plot. This analysis did not investigate individual plant patterns but rather plot level patterns. Monte Carlo permutation tests were performed to determine if observed patterns differed from random.

Results

In the fortress there are approximately 194 vegetated walls. Wall sections ranged in height from 2–10 m in height and 1–50 m in length. The largest and tallest walls are those comprising the outside of the fortress. Stone construction predominated. Many of the stone walls had been whitewashed at some point in the past. Wood and brick do occur in small amounts within many walls. Smooth walls composed of modern materials, usually cement, rarely contain plants. Likewise, most vegetated walls were considered "old" being composed of Ottoman and Byzantine building materials, although they may have been whitewashed more recently or had minor repairs consisting of various materials. The outside walls were >50 m to an opposing wall or building whereas inside walls varied from 1.65–9.00 m in distance to the opposing wall. Vegetation plots did not go above 3 m in height, however, careful examination of higher portions of the walls indicated that vegetation patterns above 3 m were similar to those that occurred at 2–3 m.

A total of 59 plant species were detected on the walls. In the 71 plots, 2786 plants of 35 species were measured (Table 1 & 2). Eleven species comprised 93.8% of the vegetation. The average density was 5.3 plants/m^2 ranging from 0.1 plants/m^2 (1 plant in 9 m^2) to 70.3 plants m^2. Except for two non-native species all of the observed species were native.

The MANOVA found significant differences between the 11 most common species based on the combined dependent variables $F(40,10412) = 82.605$, $p < 0.0005$; Pillai's Trace = 0.964; partial $\eta^2 = 0.241$, $p < 0.0005$. Post hoc tests illuminate the significant differences in height on the wall, crevice depth, aspect, and distance to the opposing wall between species (Figures 1a–d). *Cardamine hirsuta*, *Oxalis corniculata* and *Parietaria judaica* grew at lower heights on the walls and *Antirrhinum majus* and *Hordeum murinum* grew at the greatest heights. *Hordeum murinum*, *Umbilicus rupestris* and *Sedum acre* occurred in the shallowest crevices whereas *Stellaria media* and *Antirrhinum majus* were found in the deepest crevices. *Stellaria media* and *Hordeum murinum* were generally found on less exposed walls (north and east) whereas *Cardamine hirsuta*, *Allosorus acrosticus* and *Oxalis corniculata* were found on walls with more southerly aspects. *Stellaria media* and *Umbilicus rupestris* were found on walls closest to the opposing wall and *Oxalis corniculata* and *Micromeria juliana* were found on walls that were the furthest from the opposing wall.

Table 1: The 59 vascular plant species detected on the fortress walls in Elbasan, Albania. The first 35 are in order from most common to least common in the plots. The last 24 species were not observed in the sampled plots. With the exceptions of *Conyza canadensis* and *Melia azedarach* the species are all native. Seedlings of unknown Asteraceae species were also observed on the fortress walls.

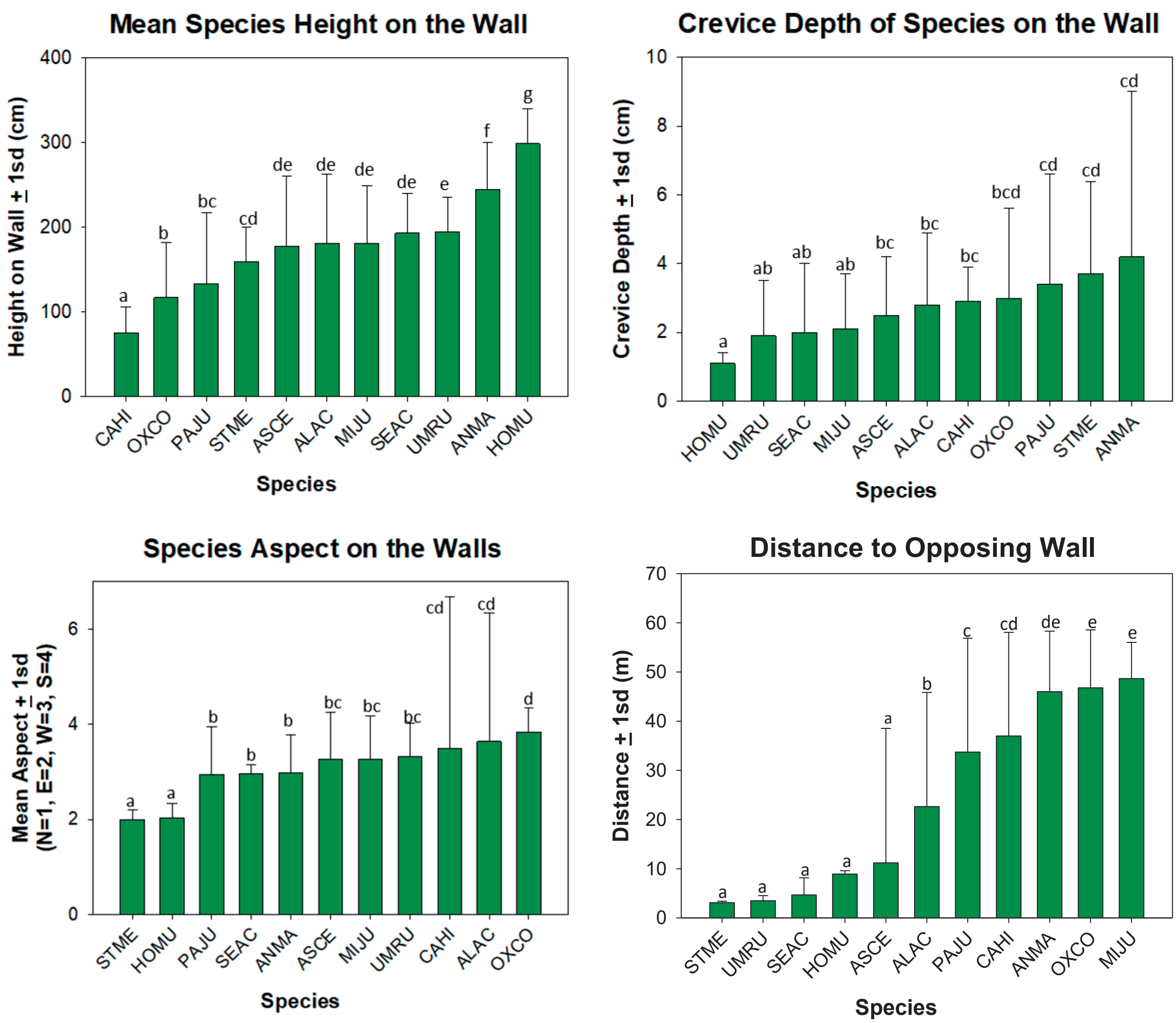
Tabela 1: 59 rastlinskih vrst, zabeleženih na zidovih trdnjave v Elbasanu v Albaniji. Prikazanih je prvih 35 vrst – od najbolj pogoste do najbolj redke na raziskovalnih ploskvah. Zadnjih 24 vrst na popisnih ploskvah nismo zabeležili. Z izjemo vrst *Conyza canadensis* in *Melia azedarach* so vse vrste domorodne. Na zidovih smo opazili tudi klice neznane vrste iz družine Asteraceae.

Species and Family – present in the plots		Species and Family – observed on the fortress walls but not in the plots
Parietaria judaica (Urticaceae)	*Ficus carica* (Moraceae)	*Adiantum capillus-veneris* (Polypodiaceae)
Allosorus acrosticus (Pteridaceae)	*Sanguisorba minor* (Rosaceae)	*Agrostis capillaris* (Poaceae)
Hordeum murinum (Poaceae)	*Lamium purpureum* (Lamiaceae)	*Allium ampeloprasum* (Amaryllidaceae)
Sedum acre (Crassulaceae)	*Arenaria serpyllifolia* (Caryophyllaceae)	*Anagallis arvensis* (Primulaceae)
Umbilicus rupestris (Crassulaceae)	*Conya canadensis* (Asteraceae)	*Apera spica-venti* (Poaceae)
Asplenium ceterach (Aspleniaceae)	*Hypericum perfoliatum* (Hypericaceae)	*Campanula ramosissima* (Campanulaceae)
Micromeria juliana (Lamiaceae)	*Poa annua* (Poaceae)	*Campanula patula* (Campanulaceae)
Cardamine hirsuta (Brassicaceae)	*Daucus carota* (Apiaceae)	*Capsella bursa-pastoris* (Brassicaceae)
Oxalis corniculata (Oxalidaceae)	*Hedera helix* (Araliaceae)	*Carex* sp. (Cyperaceae)
Antirrhinum majus (Plantaginaceae)	*Senecio vulgaris* (Asteraceae)	*Chenopodium album* (Chenopodiaceae)
Stellaria media ssp. *media* (Caryophyllaceae)	*Trifolium dubium* (Fabaceae)	*Clematis vitalba* (Ranunculaceae)
Sonchus asper ssp. *glaucescens* (Asteraceae)		*Lathyrus aphaca* (Fabaceae)
Mercurialis annua (*Euphorbiaceae*)		*Malva sylvestris* (Malvaceae)
Geranium purpureum (Geraniaceae)		*Medicago sativa* (Fabaceae)
Geranium rotundifolium (Geraniaceae)		*Melia azedarach* (Meliaceae)
Calystegia sepium (Convolvulaceae)		*Plantago* sp. (Plantaginaceae)
Convolvulus arvensis (Convolvulaceae)		*Sedum dasyphyllum*
Potentilla reptans (Rosaceae)		*Setaria pumila* (Poaceae)
Verbascum thapsus (Scrophulariaceae)		*Stachys recta* (Lamiaceae)
Fumaria officinalis (Papaveraceae)		*Taraxacum officinale* (Asteraceae)
Galium aparine (Rubiaceae)		*Thymus longicaulis* (Lamiaceae)
Veronica persicaria (Plantaginaceae)		*Trifolium repens* (Fabaceae)
Digitaria ischaemum (Poaceae)		*Urtica dioica* (Urticaceae)
Rubus fruticosus (Rosaceae)		*Viola odorata* (Violaceae)

Table 2: The 14 most common plant species, with >10 occurrences, detected on the fortress walls in Elbasan, Albania. The number of individuals is the total number of individuals encountered in all of the plots combined and the % is the percentage of the total number of plants comprised by that species. The top 11 species were used in data analysis. Except where indicated dispersal is based on our observations of the vegetation.

Tabela 2: 14 najbolj pogostih rastlinskih vrst, ki so bile prisotne najmanj desetkrat na zidovih trdnjave v Elbasanu, Albanija. Število osebkov je število vseh osebkov na ploskvah, odstotek pa predstavlja delež osebkov posamezne vrste. Enajst najbolj pogostih vrst smo uporabili v analizi. Način razširjanja je določen na podlagi naših opažanj, razen kjer je označeno z zvezdico.

Species and abbreviation	Number Individuals	%	Life form	Dispersal
Parietaria judaica PAJU	1171	42.0	perennial forb	ants, wind, water (Brandes, D. pers. comm. 2020)
Allosorus acrosticus ALAC	514	18.4	fern	wind, rhizomes, gravity, water, animal occasionally
Hordeum murinum HOMU	213	7.6	annual graminoid	animal
Sedum acre SEAC	199	7.1	perennial forb	rhizomes, stem fragments
Umbilicus rupestris UMRU	114	4.1	perennial forb	wind, leaf cutting
Asplenium ceterach ASCE	103	3.7	fern	wind, rhizomes, gravity, water, animal occasionally
Micromeria juliana MIJU	91	3.3	deciduous shrub	ballistic dispersal, animal
Cardamine hirsuta CAHI	68	2.4	annual-biennial forb	ballistic dispersal
Oxalis corniculata OXCO	56	2.0	annual-perennial forb	ballistic dispersal, rooting at nodes
Antirrhinum majus ANMA	51	1.8	annual-perennial forb	gravity dispersal
Stellaria media ssp. *media* STME	34	1.2	annual-perennial forb	ballistic dispersal, stem fragments, ants
Sonchus asper ssp. *glaucescens*	24	0.9	annual-biennial forb	wind, mammals, birds
Mercurialis annua	19	0.7	annual forb	water, ants, mammals, birds
Geranium purpureum	14	0.5	annual forb	ballistic dispersal



Figures 1a–d: The 11 most common species on the Elbasan fortress walls and their distributions across four habitat variables. See Table 2 for the species codes. Different letters across the species signify significant differences between species at $p < 0.05$ (MANOVA followed by Games-Howell post-hoc test).

Slike 1a–d: Enajst najbolj pogostih vrst na zidovih trdnjave v Elbasanu in njihova razširjenost glede na štiri rastiščne spremenljivke. Glej Tabelo 2 za okrajšave vrst. Različne črke predstavljajo statistično značilne razlike med vrstami pri $p < 0.05$ (MANOVA z Games-Howell post-hoc testom).

The ordination of the wall plots by the Monte Carlo test was significant at p=0.0410, thus the relationship of plots to environmental variables is significant (Figure 2). The CCA analysis found that 26.5% of the variance in the species data is explained by the two axes. Based on the intraset correlations of the environmental variables, which are illustrated by the length of the environmental vectors, distance to opposite wall and to a lesser extent wood and aspect along axis 1, and substrate material (brick and to a minor extent stone) along axis 2 are the most important measured environmental variables in structuring the vegetation. The longest vector, distance to the opposite wall, was the most important environmental variable in determining species distributions. For example, species in the upper left hand portion of Figure 2 occurred on walls further from opposite walls, most notably on walls on the outside of the fortress which were very far from opposing walls.

Discussion

The majority of the species were herbaceous forbs, with *Paretaria judaica* being the most common species as it is on walls in other parts of Albania (Brandes 2010) and in Italy (Lisci & Pacini 1993) and Turkey (Yalcinalp & Meral 2017). The only woody species in the 14 most

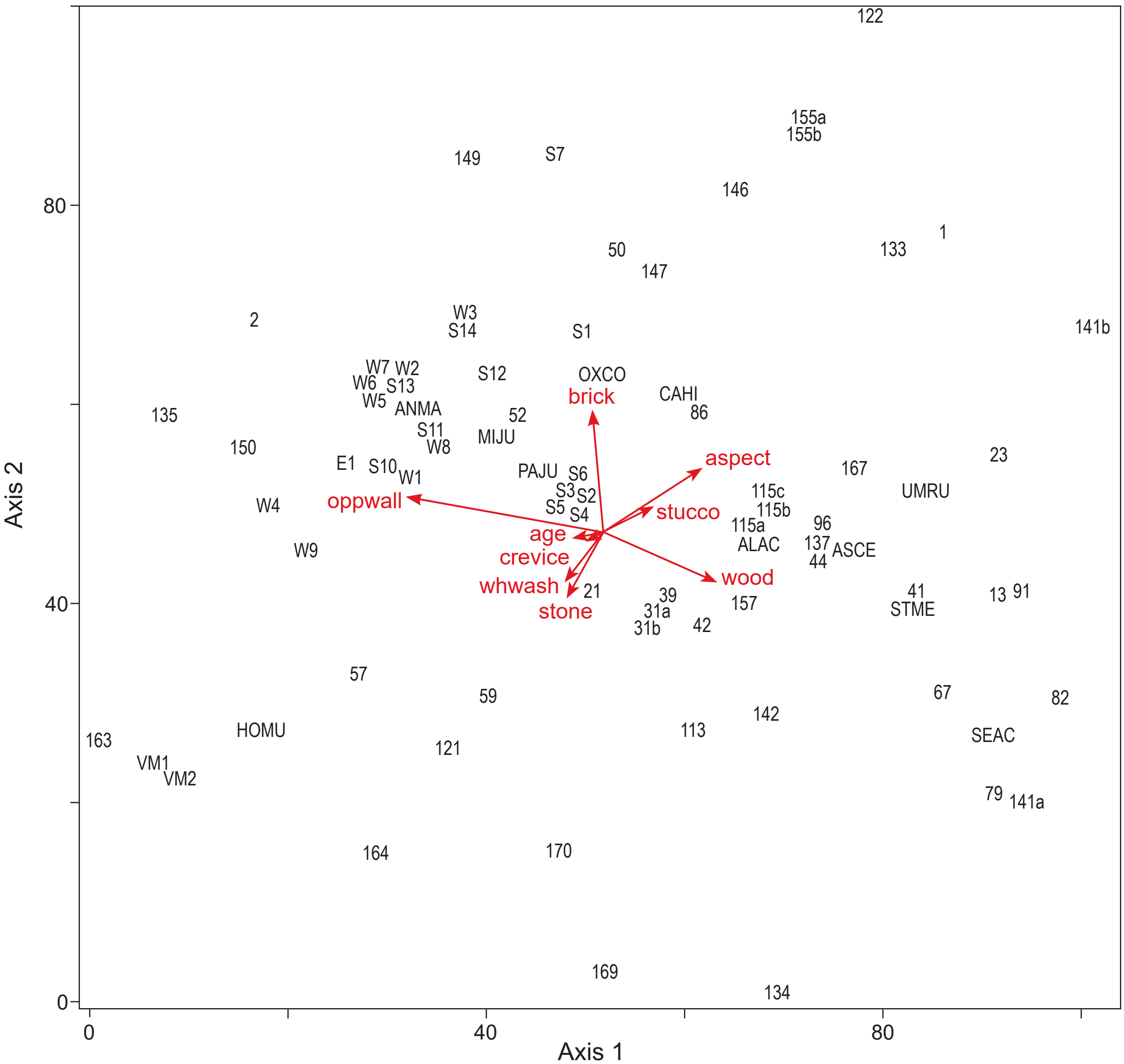


Figure 2: Canonical correspondence analysis of the Elbasan fortress wall vegetation. The 4 letter codes designate species (see Table 2) and the other codes designate plots on the walls. The vectors indicate an increasing value for that wall characteristic. The position of a species or plot relative to an environmental vector can be used to interpret the relationship between various species and plots and the measured environmental variables.

Slika 2: Kanonična korespondenčna analiza vegetacije zidov trdnjave v Elbasanu. Štiri črke predstavljajo vrste (glej Tabelo 2), ostale okrajšave predstavljajo popisne ploskve na zidovih. Puščice predstavljajo vrednosti za določeno značilnost zidu. Položaj vrste ali ploskve v odnosu do okoljskega vektorja uporabimo za razlago odnosa med različnimi vrstami, ploskvami in merjenimi okoljskimi spremenljivkami.

common species was *Micromeria juliana*, a deciduous shrub. The forbs were a mix of annual and perennial species (Table 2). Brandes (2010), Lisci and Pacini (1993) and Yalcinalp & Meral (2017) observed similar species with similar dominants as were observed in this study. Because sampling methods varied across these studies, detailed comparisons are difficult. Based on species composition, the vegetation of the walls in this study would fall into the *Galio valantiae-Parietarion judaicae* vegetation alliance (Jasprica et al. 2020).

The seeds of all of the most common species can at least potentially be dispersed by wind, although this may not be the major dispersal mechanism for species such as *Parietaria judaica* which is dispersed both by ants and wind, *Hordeum murinum*, which is more commonly dispersed by animals, and *Oxalis corniculata,* which utilizes ballistic dispersal (Table 2). In any case, it is possible that species are established initially via wind dispersal and then local dispersal may utilize other methods. For example, for species such as *Cardamine hirsuta* and *Micromeria juliana* initial establishment may be high up on a wall and further dispersal will be to crevices lower on the wall via gravity. Due to similarities in species composition dispersal characteristics are most likely similar to wall species at other Mediterranean sites (Lisci & Pacini 1993). Lisci & Pacini (1993) state that ant–dispersed species were not common on the walls in three Italian cities. The primary mode of dispersal for *Parietaria judaica* on the Elbasan fortress walls, by wind or by ants, is unknown. As would be expected, walls located further north are vegetated by different species and these species exhibit different dispersal characteristics with ant-dispersed species being the most common (Láníková & Lososová 2009, Lososová & Láníková 2010). It may be that the intensely urban environment of the Elbasan fortress has caused a reduction in ant populations thereby reducing the role of ant dispersal (Buczkowski & Richmond 2012).

Of the most common species, several may spread by asexual means from crevice to crevice on a wall by stem fragments for species such as *Sedum acre* and *Stellaria media* and by rooting at the nodes for *Oxalis corniculata*. In addition, *Allosorus acrosticus* and *Asplenium ceterach* may spread by rhizomes. This would help these species dominate portions of walls with favorable habitats, which would also greatly increase stem densities.

None of the species documented are planted as ornamentals except for *Antirrhinum majus*. Although this species was not observed in any of the few gardens in and around the fortress it may have been present as an ornamental. Many of the species were observed growing in vacant lots inside the fortress. The dominance by native species in this study is similar to walls elsewhere in the Mediterranean (Lisci & Pacini 1993, Celesti-Grapow et al. 2006) but different than walls in northern Europe where non-natives were common (Láníková & Lososová 2009). It may be that the Mediterranean flora is more adapted to harsh wall conditions. Ruderal species in Elbasan have potentially been occupying disturbed environments since the iron age, which has created long-term selection for tolerance of human-induced disturbances and thereby making this Mediterranean vegetation less prone to non-native invasions (Groves & di Castri 1991, Naveh & Vernet 1991).

The 11 most common species assort themselves nonrandomly on the walls of the Elbasan fortress (Figure 1). Species occur at significantly different heights, crevice depths, and wall aspects and are found on walls that occur at variable distances to other walls. These effects are quite powerful. The height effect may be due to dispersal mechanisms, and soil, moisture and light availability. At lower wall heights, dispersal may be easier for species that have less well-developed wind dispersal and may also be advantageous to species that potentially are dispersed by ants such as *Parietaria judiaca*. A crevice lower on a wall may contain more soil, be moister from water moving down a wall surface, and would be shadier and hence with a less intense thermal regime compared with a location higher on a wall, particularly if the wall was south facing (Lisci & Pacini 1993). Likewise, a wall closer to an opposing wall may have a less intense thermal regime due to shading compared with a wall that is distant from an opposing wall, that is, walls close to opposing walls are more likely to be shaded. Aspect is clearly important because the already stressful conditions of the walls due to difficult harsh substrates and xeric conditions are exacerbated by more intense sun exposure. A deeper crevice may be moister, have greater accumulation of soil, and may have a superior ability to capture and hold a seed than a shallower crevice.

From the CCA it can be inferred that species are widely distributed across the multivariate space, that is, different species are found on different wall habitats (Figure 2). Several of the habitat variables are weakly correlated with the species distributions, which can be seen by their low intraset correlations (not shown) and short vectors (age, crevice, whitewash and stucco). Most of the walls are made of stone, which is why this factor is weak, i.e., all of the species occur on stone walls. Few of the walls contain large amounts of brick or wood but these two variables are important in species distributions. Walls covered with stucco contained few species. The age of the wall or how recently the wall had been whitewashed were not important in species distributions. Crevice depth on the CCA is based on a plot average, which is not important in structuring plant distributions, whereas in the MANOVA crevice depth was analyzed on a per plant basis, and showed significant differences between plant species inhabiting crevices of different depths.

On the CCA it can be seen that *Allosorus acrosticus, Asplenium ceterach, Umbilicus rupestris, Stellaria media,* and especially *Sedum acre* preferred walls which were closer to the opposing wall and commonly contained wood. *Antirrhinum majus* and *Micromeria juliana* preferred walls located farther from opposing walls and that generally contained brick; these were the walls on the outside of the fortress. *Oxalis corniculata* and *Cardamine hirsuta* occurred more often on brick walls with southerly aspects. *Hordeum murinum* occurred on east and north facing walls further from opposing walls, which describes walls VM1 and VM2 where much of the *Hordeum murinum* occurred. On VM1 and VM2 there were a series of long shallow crevices with dense stands of *Hordeum murinum*. *Parietaria judaica* was located close to the centroid, which indicates that it occurs equally in a wide variety of habitats.

The reasons for the preferences for certain substrates, such as wood and brick, is difficult to determine. It can be assumed that species on southerly aspects, and to a lesser extent on walls distant from the opposing wall, are tolerant of greater exposure. However, these two vectors are facing nearly in opposite directions because north and east facing walls are more often farther from an opposing wall. Using the CCA and Figures 1c and 1d, exposure tolerances of the species may be examined. In Figure 1c, aspect differences between species are not large although significant differences occur. *Oxalis corniculata*, *Allosorus acrosticus* and *Cardamine hirsuta* occur on more southerly aspects in both Figure 1c and in the CCA (Figure 2). We conclude that these species would be the most exposure tolerant, especially *Oxalis corniculata* because it typically occurs on walls farther from opposing walls than do the other species (Figure 1d). A species such as *Umbilicus rupestris*, which also occurs on south aspects but on walls close to opposing walls, would most likely be less exposure tolerant. *Stellaria media* occurs on north aspects on walls located close to an opposing wall, suggesting this species is relatively intolerant of exposure.

It is important to keep in mind that 73.5% of the pattern is unexplained by the first two axes. Random initial establishment, which leads to a population of a species being present, could lead to there being a large stochastic element in the distribution.

Differences in mortar composition and how mortars of different time periods may differ were not tested in this study. Mortar is alkaline in composition, which would function as an important species filter (Lisci & Pacini 1993).

These walls are an important repository for urban biodiversity. Urban areas often have very few habitats, so walls which support high species richness can be important habitats. With the replacement of walls rich in crevices with modern stucco and concrete walls, these species are at risk thereby reducing the stability of urban biodiversity dramatically.

Acknowledgements

We are indebted to the following Universiteti 'Aleksander Xhuvani' students: K. Hoxholli, K. Velillari, E. Xharo, A. Rapi, K. Merzheku, R. Hasanllari, G. Toçka, D. Dama, E. Qorraj, and professors: B. Pupuleku, N. Kallajxhiu, S. Turku, who measured many plants on the fortress walls. Thank you to D. Stanford and M. Truong who also measured many plants. Thank you to S. Mali who made this study possible and to a Fulbright Scholarship to J. Titus for funding. Two reviewers greatly improved the manuscript.

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