Short communication

Mounding alters environmental filters that drive plant community development in a novel grassland

Nate Hough-Snee*, A. Lexine Long1, Lacey Jeroue, Kern Ewing

University of Washington Center for Urban Horticulture and School of Forest Resources, Box 352100 Seattle, WA 98195-2100, United States

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ABSTRACT

Earthen mounds are commonly used in ecological restoration to increase environmental heterogeneity, create favorable microclimates and retain soil resources that promote plant establishment. Although mounding is commonly employed in restoration, few microtopography studies focus on the long-term effects of mounding on restored plant community development. We assessed the vegetation and physical environment of earthen mounds installed at a novel grassland ten years after restoration to look for patterns in plant community development. We used permutational multiple analysis of variance (PERMANOVA) to identify differences in plant community composition and the associated mound-driven environmental variables, summer soil moisture and height above peak soil inundation, in relation to mound position. We used indicator species analysis (ISA) to classify the species that defined mound top and intermound space plant communities. We found that mound position drove plot height above flooding and soil moisture while plant community composition was driven by plot height above flooding, summer soil moisture, and mound position. ISA showed that species colonized mound microsites differently: most wetland species occurred between mounds and xeric stress tolerators largely occupied dry mound tops. We visualized these differences with non-metric multidimensional scaling (NMDS) ordination, finding that species sorted out in multivariate space based on mound position. We conclude that mounding can have relatively long-term effects on plant community development, even in highly disturbed, minimally maintained restoration projects.

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1. Introduction

Earthen mounds create diverse microtopography that affect soil moisture, light availability and nutrient cycling that can drive vegetation establishment and survival in a variety of ecosystems (Bruland and Richardson, 2005; Ewing, 2002a; Moser et al., 2007; Werner and Zedler, 2002). Accordingly, mounding is commonly employed within restoration projects to emulate natural microtopographic features and alter the availability of resources that may allow diverse vegetation to establish (Ewing, 2002a; Rossell et al., 2009; Simmons et al., 2011; Whisenant, 1998). Mounding has been shown to increase the establishment, survival, and diversity of seeded and planted vegetation on landfill caps (Biederman and Whisenant, 2011; Ewing, 2002a), increase plant species richness in restored wetlands (Bruland and Richardson, 2005; Moser et al., 2007) and drive plant community development in passively restored and planted wetlands (Rossell et al., 2009; Simmons et al., 2011) shortly after restoration. The decline of microtopography-forming tussocks in sedge meadows has been correlated to declines in native plant abundance (Werner and Zedler, 2002) while microtopographic variability has also been correlated to plant community composition in novel roadside ecosystems (Karim and Mallik, 2008) and seed bank development on grazed ski runs (Isselin-Nondedeu and Bédécarrats, 2007). While mounding is widely used in restoration and has shown very clear short-term effects on vegetation establishment, very few studies have examined how the effects of mounding may persist over longer timeframes in restored sites at the plant community level.

To see how mounding affected plant community development 10 years after restoration, we assessed plant community composition and environmental filters at a restored novel grassland ecosystem that used created microtopography to facilitate plant colonization and survival. This study had three primary objectives: (1) to estimate how the environmental filters of soil flooding and drying changed across mounds in the restored environment, (2) to

* Corresponding author. Present address: Utah State University Ecology Center and Watershed Sciences Department, 5210 Old Main Hill, Logan, UT 84322-5210, United States.

E-mail addresses: nwhs@uw.edu, nathoughsnee@gmail.com (N. Hough-Snee).

1 Present address: King County Noxious Weeds Program, 201 South Jackson Street, Seattle, WA 98104, United States.
Table 1

| Hypothesis and dependent variables from PERMANOVA models | Hypothesis 1: mound height above OHWM | Hypothesis 2: soil moisture | Hypothesis 3a: community composition | Hypothesis 3b: percent wetland vegetation | Hypothesis 3c: percent native vegetation |
|----------------------------------------------------------|--------------------------------------|-----------------------------|--------------------------------------|------------------------------------------|------------------------------------------|
| Independent variables from PERMANOVA models              | Mound position                       | Aspect                      | Soil moisture                         | Mound height above OHWM                  | OHWM × mound position                   |
|                                                          | 17.854 (0.0001)*                     | 15.17 (0.0001)*             | 20.16 (0.0001)*                      | 21.29 (0.0001)*                          | 6.484 (0.0132)*                        |
|                                                          | 0.13 (0.7759)                       | 0.32 (0.7929)               | 0.10 (0.9331)                        | 0.66 (0.5138)                            | 2.530 (0.2052)                         |
|                                                          | 2.68 (0.1690)                       | 7.01 (0.0010)*              | 2.03 (0.1390)                        | 1.33 (0.3629)                            | 1.663 (0.1530)                         |
|                                                          | 4.13 (0.0022)*                      | 1.46 (0.1109)               | 1.75 (0.1925)                        | 4.4 (0.0011)                             | 2.178 (0.140)                          |
|                                                          | 3.40 (0.0010)*                      | 4.4 (0.0011)                |                                      |                                          |                                          |

* P < 0.05.

Table 1 presents F-values and P-values (in parentheses) for factors (rows) used in hOHWM and soil moisture, vegetation community composition, wetland vegetation and native vegetation PERMANOVA analyses.

We hypothesized that mound topography filters vegetation by modifying the physical environment: flood-tolerant wetland species, both native and non-native, would be most abundant in the wet intermound spaces while drought-tolerant, native graminoids and forbs would dominate resource-depaupeaer mound tops.

2. Site history

The site we assessed is the former E-5 parking lot on the Union Bay Natural Area (herein UBNA; Seattle, WA), a 30-ha former landfill that was capped with clay and gravel, graded and seeded with non-native pasture grasses in 1971. The UBNA consists of several grassland and wetland ecotones, most of which suffer from several limitations to natural, native plant colonization, including low soil nitrogen and organic matter (Ewing, 2002b), low summer soil moisture (Ewing, 2002b) and abundant invasive species in areas with high levels of soil resources (Ewing, 2007; Hough-Snee et al., 2011). Due to subsidence and shifting of capped landfill materials, E-5 persists as a basin that fills with water during winter rains, holding open water through early summer until the site dries out completely (Ewing, 2002a). Like many highly altered ecosystems, the UBNA has a short ecological memory—cumulative within site biological legacies and pressures from the surrounding matrix (e.g. Schaeffer, 2009)—that prevent returning the landscape to the historic palustrine wetland ecosystem that existed pre-landfill. Because non-native soils, abundant weeds, and novel hydrology compromise site ecological memory to drive vegetation across UBNA, the most common restoration goal across UBNA is to attain self-sustaining plant communities governed by autogenic processes rather than human maintenance (Whisenant, 1998).

To create a heterogenous environment more conducive to plant establishment, in 1998 the E-5 parking lot was disked and tilled, mounds were created and native prairie vegetation was installed. 108 mounds were created in the 1.5-ha E-5 area by piling gravel and cap material into circular features. Each mound was amended with a small amount of topsoil, and evenly planted with native prairie plants (annotated in Table 2). After initial construction, mounds ranged in height from 40–70 cm with base widths of 50–70 cm. The interaction between substrate, precipitation and E-5’s subsiding, mound topography exposes plants to flooded or saturated conditions during the early part of the growing season and extremely dry conditions late in the growing season. Pasture grasses from upslope at UBNA have spread into E-5 following restoration, but with the exception of invasive Himalayan blackberry (Rubus armeniacus) removal, plots have received no maintenance since restoration.

3. Methods

In July 2008, we randomly selected and relocated 30 of the restored mounds. Four rectangular 1/2 m² plots were established on each mound, two on top of each mound and two in the adjacent intermound spaces. Plots were placed lengthwise from west to east and were stratified by aspect, for a total of 120 plots. This sampling scheme provided a treatment structure equivalent to a blocked 2 × 2 factorial design with two mound positions, mound top or intermound space and two aspect treatments, north or south within each block. We estimated the relative abundance of all vascular plants in each plot in the first two weeks of July 2008. Species in each plot were pooled by wetland indicator status (USFWS, 1996) and then separately for their native status in Washington State (NRCS, 2010). Plant species were considered wetland indicators if their wetland status ranged between OBL and FACW. All plants with other wetland indicator statuses were considered non-wetland plants. On July 28, 2008 we measured volumetric water content at 12 cm within each plot using a Hydrosense CS-620 soil moisture probe (Campbell Scientific, Logan, UT, USA).

We delineated the ordinary high water mark (OHWM; Olson and Stockdale, 2010), within E-5 to define the high point at which surface water pools during the rainy season and installed a temporary benchmark from which we measured mound height above OHWM (hOHWM). We surveyed the height of each relocated mound with a standard level and rod (Nikon AC-2s, Nikon, Westminister, CO, USA) and calculated the difference between each surveyed plot height and the surveyed OHWM benchmark to yield a single hOHWM measurement for each plot. OHWM is a strong indicator of the normal elevation at which standing water creates wetland soil properties and is used in the delineation of wetlands.
in Washington State. We used hOHWM as a proxy for the depth and duration of flooding experienced at each plot where the higher the hOHWM for a plot, the less flooding stress we considered the plant community within that plot to incur.

4. Data analysis

We used PERMANOVA, a permutation-based ANOVA procedure that uses pseudo-\(F\)-tests on distance matrices to assess differences between multivariate or univariate groups (Anderson, 2001), to test our groups of hypotheses. For hypothesis 1a, we used a one-way model with mound position as the only factor. For hypothesis 1b, we used a two-way model with mound position and aspect as factors. For hypotheses 2a, 2b and 2c, the full model included mound position, aspect, hOHWM, soil moisture and the interaction terms between hOHWM and mound position and between soil moisture and mound position. Block (mound) effects were included to account for additional error variability within the model (Oehlert, 2000). All PERMANOVA analyses used Bray–Curtis distance and 10,000 permutations constrained within each block (Anderson and ter Braak, 2003) to assess statistical significance. For community-level analyses we removed species from the data that occurred in less than 5% of plots (McCune and Grace, 2002). We used all surveyed species to calculate the proportions of obligate wetland and native vegetation present in each plot. There were one Agrostis species and one Bromus species that could be identified only to the genus level and are referred to as Agrostis sp. and Bromus sp. in our analyses.

We visualized the vegetation community using non-metric multidimensional scaling (NMDS) and used indicator species analysis (Dufrene and Legendre, 1997) to identify species that were strongly representative of a given mound position. Indicator species analysis (ISA) serves to illustrate unique species within groups as a product of the relative abundance and relative frequency of a given species within a given group (Dufrene and Legendre, 1997; Bakker, 2008). ISA provides an indicator value of 0–100 for each species, with a perfect indicator value being 100 and a non-indicator being close to zero. Species whose indicator value for a given mound position yielded a \(P\)-value <0.05 when compared to 10,000 Monte Carlo randomizations of the full data set were considered significant indicators. All analyses were performed in the R statistical package version 2.11.1 (R Development Core Team, 2010).

5. Results and discussion

Position on a given mound—mound top or intermound—drove both vegetation and soil moisture parameters (Table 1). The mean summer soil moisture for intermound plots was 5.4% (range = 5–9%) while mean soil moisture on the higher mound top plots was 4.1% (range = 3–8%, \(P=0.0004\); Fig. 1). This trend was consistent with the average hOHWM by mound position, \(-0.004\) m on the mound tops (range = \(-0.35\) to \(-0.71\) m) and \(-0.174\) m (range = \(-0.51\) to \(-0.66\) m) on the intermound plots (\(P<0.0001\); Fig. 1).

Mound and intermound vegetation communities were comprised of 67 vascular plant species and differed by mound position \(P=0.0001\) while soil moisture and hOHWM also had significant effects (Table 1). Post hoc PERMANOVA comparisons between groups showed that the plant composition of mound tops differed from intermound plots regardless of aspect \(P<0.0001\) for all comparisons). The intermound spaces yielded higher proportions of wetland plant species (14%) than the mound tops (1.9%;

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Table 2. Indicator species returned from indicator species analysis using mound position as the treatment. We also report wetland indicator status, plant native status and four letter plant codes. Species in bold font were seeded during 1998 restoration. Wetland status is based on US Fish and Wildlife Service wetland indicator category: OBL, obligate wetland; FACW, facultative wetland; FAC, facultative; FACU, facultative upland; NI, no indicator (USFWS, 1996). Species nomenclature follows USDA PLANTS database (NRCS, 2010).

| Plant species               | Species code | Treatment | Indicator value | Probability | Wetland status | Native status | Plant functional type |
|-----------------------------|--------------|-----------|----------------|-------------|----------------|---------------|-----------------------|
| Daucus carota               | DACA         | Mound     | 71.05          | 0.0001*     | UPL            | Non-native    | Forb                  |
| Trifolium dubium            | TRDU         | Mound     | 52.55          | 0.0001*     | UPL            | Non-native    | Forb                  |
| Vicia sativa                | VISP         | Mound     | 39.15          | 0.0001*     | UPL            | Non-native    | Forb                  |
| Holcus lanatus              | HOLA         | Mound     | 35.39          | 0.6005      | FAC            | Non-native    | Graminoid             |
| Potentilla gracilis         | POCR         | Mound     | 33.86          | 0.0008*     | FAC            | Native        | Forb                  |
| Plantago lanceolata         | PLLA         | Mound     | 32.67          | 0.001*      | FAC            | Non-native    | Forb                  |
| Fragaria virginiana         | FRVI         | Mound     | 27.92          | 0.0177*     | FACU           | Native        | Forb                  |
| Festuca bromoides           | FEBR         | Mound     | 25             | 0.0005*     | Ni             | Non-native    | Graminoid             |
| Festuca idahoensis var. roemeri | FEID       | Mound     | 20.41          | 0.0258*     | FACU           | Native        | Graminoid             |
| Symphoricarpos alba         | SYAL         | Mound     | 16.67          | 0.0018*     | FACU           | Native        | Shrub                 |
| Festuca rubra               | FERP         | Mound     | 16.19          | 0.0062*     | FAC+           | Non-native    | Graminoid             |
| Anthoxanthum odoratum       | ANOD         | Mound     | 14.55          | 0.9298      | FACU           | Native        | Graminoid             |
| Juncus bufonius             | JUBU         | Mound     | 14.24          | 0.0091*     | FACW           | Native        | Graminoid             |
| Hypericum perforatum        | HYPE         | Mound     | 10.73          | 0.113       | UPL            | Non-native    | Forb                  |
| Bromus mollis               | BRMM         | Mound     | 10.37          | 0.0746      | UPL            | Non-native    | Graminoid             |
| Bromus spp.                 | BRSP         | Mound     | 8.87           | 0.1084      | Ni             | Non-native    | Graminoid             |
| Rabus armeniacus            | RUAR         | Mound     | 6.67           | 0.7111      | FACU           | Native        | Shrub                 |
| Populus balsamifera         | POPB         | Mound     | 6.04           | 0.6339      | FAC            | Native        | Tree                  |
| Hypochoeris radicata        | HYRA         | Mound     | 4.24           | 0.6948      | FACU           | Non-native    | Forb                  |
| Phalaris arundinacea        | PHAR         | Mound     | 3.08           | 1.0         | FACW           | Non-native    | Graminoid             |
| Agrostis stolonifera        | AGST         | Intermound| 44.72          | 0.0001*     | FAC            | Non-native    | Graminoid             |
| Schiedanorus pratensis      | SCPR         | Intermound| 35.27          | 0.0026*     | FACU           | Native        | Graminoid             |
| Agrostis tenus              | AGTE         | Intermound| 34.39          | 0.0003*     | FAC            | Non-native    | Graminoid             |
| Eleocharis palustris        | ELPA         | Intermound| 30.64          | 0.0004*     | OBL            | Native        | Graminoid             |
| Trifolium pratense          | TRPR         | Intermound| 24.52          | 0.0088*     | UPL            | Non-native    | Forb                  |
| Lotus corniculatus          | LOC0         | Intermound| 21.33          | 0.0036      | FAC            | Non-native    | Forb                  |
| Melilotus alba              | MEAL         | Intermound| 13.33          | 0.0071*     | FACU           | Non-native    | Forb                  |
| Chichoryi intybus           | CIIN         | Intermound| 13.23          | 0.3418      | UPL            | Non-native    | Forb                  |
| Agrostis spp.               | AGSP         | Intermound| 10.17          | 0.3555      | Ni             | Non-native    | Graminoid             |
| Juncus accuminatus          | JUAC         | Intermound| 10.00          | 0.0289*     | OBL            | Native        | Graminoid             |
| Achillea millefolium        | ACM1         | Intermound| 8.12           | 0.5525      | FACU           | Native        | Forb                  |
| Lythrum salicaria           | LYS1         | Intermound| 8.08           | 0.2762      | FACW           | Non-native    | Forb                  |
| Leucanthemum vulgare        | LEUV         | Intermound| 8.00           | 0.2463      | Ni             | Non-native    | Forb                  |
| Parentucellia viscosa       | PAVI         | Intermound| 5.33           | 0.4802      | FAC-           | Non-native    | Forb                  |

* Species that were statistically significant indicators (10,000 permutations).

$P = 0.001$ for mound position). Mound tops showed a higher mean proportion of native vegetation (24.5%) than the intermound spaces (20.2%; $P = 0.013$ for mound position). NMDS ordination returned a three dimensional solution with a stress of 13.73 ($P = 0.0099$, 10,000 permutations) and an $R^2$ of 0.915 (Fig. 2). There were 24 species that significantly affected the ordination results ($P < 0.05$) and both plots and species appeared to sort by mound position and hOHWM (NMDS axis 1; Fig. 2).

IBA returned 11 and 8 statistically significant indicator species for mound tops and intermounds respectively (Table 2). The strongest indicator species for the intermound treatment were either facultative or obligate wetland graminoids whereas the mound top indicator species were largely upland forb species. The strongest native indicator species for mound tops included Festuca idahoensis var. roemeri, Fragaria virginiana and Potentilla gracilis, all species adapted to drought stress and considered stress tolerant. We anticipated that these native species would compete with weedy forbs that exploit soil resources, but this did not occur: the strongest overall mound top indicators were non-native forbs—Daucus carota, Trifolium dubium and Vicia sativa—with large taproots that may enhance resource acquisition. Eleocharis palustris, a flood-tolerant, native wetland species, and the non-native facultative species Agrostis stolonifera and Schiedanorus pratensis thrived in the more deeply flooded intermound spaces. The strongest intermound indicators—A. stolonifera, S. pratensis and Agrostis tenus—were all graminoids with plastic tendencies to both flooding and drying. The observed indicator species suggest that

![Fig. 2. The first two axes from the NMDS ordination for the vegetation community show a distinct grouping between the plant communities encountered on the tops of mounds and the adjacent intermound spaces. Species loading vectors with a $P$-value $<0.1$ (10,000 permutations) are plotted over sites although we found 24 significant species at $P = 0.05$. Four letter species codes correspond to those used in Table II. NMDS stress = 13.7303 and linear $R^2 = 0.912.$](https://example.com/fig2.png)
plant success and around microtopography is a product of species' ability to endure flooding or drought that drive distinct assemblages by mound position and total onsite plant diversity.

6. Conclusions

Mounding facilitated distinct differences in environmental filters and plant functional diversity ten years after restoration of a former parking lot to grassland. Both mound positions experience dry summer soils and are at least partially inundated in winter, but the drier, higher mound tops exhibited higher average hOHALM and lower summer soil moisture that filtered the plant community towards more native, drought-tolerant forbs and graminoids and less flood-tolerant wetland species than the intermound areas. These long-term results are supported by studies that document the short-term effects of mounding on the success of planted and seeded grassland and forest vegetation (Biederman and Whisenant, 2011; Ewing, 2002a; Simmons et al., 2011) and wetland vegetation recovery following disturbance (Anderson et al., 2007; Vivian-Smith, 1997). Our results also corroborate observations that decreased soil moisture and higher microtopographic elevations correlate to increased stress-tolerating, native plant composition in other novel plant communities (Karim and Malik, 2008).

While achieving high levels of plant functional and species diversity are common goals in reclamation and ecosystem restoration projects (Biederman and Whisenant, 2011; Zedler, 2005), site modification should be paired with adaptive vegetation management to direct full autogenic recovery of a given site. Restoration practitioners attempting to create diverse plant communities on resource-poor sites should consider engineered mounds to increase site environmental heterogeneity that provides diverse niches for plants (Vivian-Smith, 1997). Mounding facilitates long-term changes in a site's physical performance, but does not necessarily increase native species composition or yield desirable successional trajectories without further management (Whisenant, 1998). For example, in reclamation projects, landform often interacts with plant species' growth form and life strategy over relatively long timeframes to drive plant communities (Jochimsen, 2001, Rudgren et al., 2011), regardless of initial propagule introduction or soil amendment that may drive vegetation in short (Ewing, 2002b) or long timeframes (Conrad and Tischew, 2011; Hough-Snee et al., 2011). When a project objective is to increase native plant biodiversity over long timeframes rather than to create a self-sustaining novel plant community, practitioners should pair the creation of microtopographic features with invasive species management and consider introducing supplemental propagules of native plant species whose performance matches created microsites allowing them to outcompete resource efficient invasive species.

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