

RESEARCH ARTICLE

•
Testing the Efficacy
of Species Richness
and Floristic Quality
Assessment of
Quality, Temporal
Change, and Fire
Effects in Tallgrass
Prairie Natural Areas

Marlin Bowles¹

The Morton Arboretum
Lisle, Ill. 60532

Michael Jones

Christopher B. Burke Engineering, Ltd.
Rosemont, Ill. 60018

•
¹ Corresponding author:
mbowles@mortonarb.org

ABSTRACT: Despite extensive use, few studies have thoroughly tested competency of the Floristic Quality Index (FQI) to assess vegetation quality by comparing it with alternative statistics and with independent measures in large data sets. We compared the efficacy of species richness and floristic quality indices in detecting temporal change and fire effects on quality within and among tallgrass prairie remnants. We calculated species richness at small (1/4-m² plot) and large (total sample) scales, as well from a Species Richness Index (SRI) that integrates these measures. These statistics were compared with FQI, which assesses quality by integrating species richness with estimates of species conservatism (C values) to undisturbed natural vegetation. We made within-site comparisons of temporal change in dry-mesic and mesic prairie vegetation following 22 years of fire exclusion and then after five years of fire management. The among-site comparisons used 33 prairies that were graded as A or B quality and sampled in 1976 by the Illinois Natural Areas Inventory (INAI). We resampled these sites in 2001 and analyzed vegetation change in relation to their fire-management histories.

Within-site comparisons found that significant declines in average plot species richness corresponded to independent measures that documented deterioration of vegetation composition and structure. In contrast, lack of significant change in average C values failed to detect these changes. We found that species richness was greatest in mesic habitats, while C values were biased toward higher values assigned to dry prairie species. Among sites, those ranked as grade A by the INAI had greater species richness than grade B sites. Temporal changes in species richness in these sites were also positively correlated with fire frequency, which in turn was negatively correlated with a shift in vegetation structure toward increasing woody vegetation and loss of grasses. Average C values did not differ significantly between the INAI A and B quality grades, nor were they correlated with fire frequency; however, they were negatively correlated with increasing woody dominance. These results indicate that, for tallgrass prairie, measures of species richness can be very sensitive indicators of vegetation change, and can help gauge differences in vegetation quality within vegetation types. In contrast, indexing floristic quality is inconsistent and problematic due to bias and lack of precision in assigning conservatism scores as well as instability in the FQI formula and potential for circular reasoning in validating its effectiveness.

Index Terms: fire-management, Floristic Quality Index (FQI), Species Richness Index (SRI), tallgrass prairie, temporal change

INTRODUCTION

Monitoring the condition of natural vegetation is a challenging responsibility for conservation resource managers and scientists. This is especially critical for prairie vegetation, which often deteriorates with disruption of natural fire regimes (e.g., Leach and Givnish 1996, Bowles et al. 2002, Bowles and Jones 2004). Using indices to detect such change and to assess responses to management is attractive because of their potential ease of application, despite well-known problems of collapsing complex data into single measures (Magurran 1988). Most recently, this approach has led to development of the Floristic Quality Index (FQI). This index assesses quality using subjectively assigned coefficients of conservatism (C values) that usually range from 1-10 to reflect the degree to which species appear restricted to undisturbed natural vegetation (Wilhelm and Ladd 1988, Swink and Wilhelm 1994). This concept differs from ranking ecological adaptation to different habitats (e.g., Curtis

and McIntosh 1951, Curtis 1959), and is more in line with survival strategies and adaptation to different successional stages following human disturbance (Taft et al. 1997). Because of the apparent robustness of FQI (e.g., Wilhelm and Ladd 1988, Herman et al. 1997, Taft et al. 1997, Taft et al. in press), it has been assessed for use in woodlands in Ontario (Francis et al. 2000), Illinois (Bowles et al. 2000), and Wisconsin (Rooney and Rogers 2002), wetlands in Illinois (Matthews 2003), Wisconsin (Werner and Zedler 2002), Ohio (Lopez and Fennessy 2002) and Florida (Cohen et al. 2004), and for native and restored prairies in Illinois (Allison 2002, Kirt 1997, Taft et al. in press). However, the FQI formula ($FQI = \bar{x}C*\sqrt{S}$, where S = No. of species) is problematic because it combines independent qualitative and quantitative units of measure that confound statistical application and interpretation (Francis et al. 2000, Bowles et al. 2000, Rooney and Rogers 2002, Cohen et al. 2004). As a result, Rooney and Rogers (2002) and Cohen et al. (2004) suggested using only

C values to evaluate quality.

Competency of the subjectively assigned C values for Illinois (Taft et al. 1997) and for the Chicago region (Swink and Wilhelm 1994) has not been thoroughly tested by comparing them with alternative statistics and independent measures using large data sets that include temporal change and management applications. In this paper, we make such comparisons using data set matrices containing species by plot occurrences from which we calculated average plot species richness ($\bar{x}R$), the total number of species sampled (S), and a Species Richness Index (SRI) that integrates $\bar{x}R$ and S as $SRI = \bar{x}R * \ln S$, where $\ln S$ is the natural logarithm of S (Bowles et al. 2000). Although common usage often equates $\bar{x}R$ and S as measures of richness, $\bar{x}R$ represents species density per unit area while S represents species richness dependent upon sample size and area of plot dispersion (Hurlbert 1971, Magurran 1988, Rosenzweig 1995). In our comparisons of FQI and SRI, we asked: (1) how well does each gauge vegetation quality as assessed by independent methods, (2) are they sensitive to temporal change in vegetation composition and structure, (3) can they detect fire management effects on vegetation, and (4) are they capable of detecting differences at both large and small scales, such as within and among sites? We also sought to determine evidence of bias in assigning conservatism values across the landscape gradient represented by our data set, and whether C values assigned to the Chicago region (Swink and Wilhelm 1994) and to Illinois (Taft et al. 1997) differed in this respect, as well as in their effectiveness in detecting quality.

STUDY SITES

We used historic and recent data collected from natural prairie remnants in the Chicago region of northeastern Illinois. This area originally supported fire-maintained vegetation that was primarily prairie (Cowles 1901, Kilburn 1959, Moran 1978). Prairie vegetation occurred across a moisture gradient ranging from dry to wet, with sand, gravel, dolomite and silt-loam substrates (White and Madany 1981). Most mesic and

wet habitats occur on glacial till or glacial lake-bed deposits, while dry habitats are restricted to rare landscape features such as gravel kames or sand dunes (Willman 1971). More than 60 remnant prairie stands in this region were studied by the Illinois Natural Areas Inventory (INAI) in 1976, during which vegetation was classified, graded for quality, and then sampled to provide a basis for long-term monitoring (White 1978). The quality grades were based on vegetation composition and evidence of human disturbance, with grades reflecting stages of plant succession following human disturbance. Grade A represented undisturbed late-successional vegetation, grade B represented moderately disturbed mid-successional, grade C heavily disturbed early-successional, and grade D very heavily disturbed early successional (White 1978). Usually only A or B quality sites were sampled by the INAI. Our within-site comparisons used INAI data sets representing grade A dry-mesic and mesic gravel prairie in the 4.40 ha Santa Fe Prairie Nature Preserve, Cook Co., Illinois. This site is a fragment of original prairie in the Des Plaines River Valley of northeastern Illinois. We used it for comparison because it underwent severe degradation due to absence of fire until it was protected in 1998 (Bowles et al. 1998). For among-site comparisons, we used sampling data from 33 grade A and B prairie remnants that had historic fire-management records. These stands represented dry, dry-mesic, mesic and wet-mesic prairies.

METHODS

Data collection

All sampling data consisted of species presence in 20 or 30 circular 1/4m² plots placed randomly along transect lines that were located within selected plant communities. These transects and communities were mapped by the INAI on overlays of 1:7920 scale aerial photos. We resampled most prairies in 2001 by resurveying transect line locations during approximately the same time of the growing season as when they were originally sampled. The Santa Fe Prairie was resampled in 1998, and in 2003

after five years of restoration that included fire-management and herbicide application to cut stems of invading gray dogwood (*Cornus racemosa*) and the alien buckthorn *Rhamnus cathartica*. The general condition of each site was assessed during resampling, and fire-management histories were obtained from land managers. These records were assumed to be complete for the 1980-present time period, which covers > 20 years. We did not use records for the 1976-79 time period because they appeared incomplete, and represent a 4-year period that would have had comparatively little effect on the condition of vegetation that we sampled during 2001-02. Greater taxonomic precision with difficult species (e.g., *Carex* spp) in 2001 required collapsing some species into generic groups in order to avoid inflating species richness.

Independent assessments of vegetation change

To independently assess temporal change within the dry-mesic and mesic sites at Santa Fe Prairie, we compared among years the relative abundance of native and alien grass, sedge, forb, and woody plant species groups, as well as plot frequencies of individual species. For among-site comparisons we used the a priori A and B quality grade assignments made by the INAI in 1976 as independent assessments of quality. We also calculated an index of compositional structure represented by the ratio of relative abundance of woody to graminoid vegetation (= W/G ratio). This ratio is usually < 1.0, as grass and sedge species are more abundant than woody species in prairie. It increases either as woody species presence increases or as grass and sedge species presence decreases, both of which represent negative changes in prairie vegetation (Bowles and Jones 2004).

Index calculations

Species richness indices were calculated from species by plot occurrence matrices representing each site. In addition to the SRI (= $\bar{x}R * \ln S$), a Native Richness Index was calculated as: $NRI = \bar{x}R_n * \ln S_n$, where $\bar{x}R_n$ = the average number of native species per plot, S_n = the total number of native

species sampled and $\ln S_n$ = the natural logarithm of S_n . An alien index (AI) can also be calculated as the difference between SRI and NRI. The NRI and $\bar{x}R_n$, as well as S_n , are the primary species richness metrics used for comparisons in this paper. The Floristic Quality Index was calculated for each matrix using Coefficient of Conservatism (C) values for native Chicago region species (range = 0-10) from Swink and Wilhelm (1994), where $FQI = \bar{x}C * \bar{x}\sqrt{S_n}$, and $\bar{x}C = \sum_i C_i / S_n$ across all native species in each matrix. We did not combine alien and native C values, which may produce a more realistic estimate of quality (Taft et al. in press). We also calculated $\bar{x}C$ values using statewide Illinois C values from Taft et al. (1997). Because species with higher frequencies intuitively should have greater influence on FQI (Cohen et al. 2004), we also calculated weighted C values by the formula $\bar{x}C_w = \sum_i (C_i * f_i) / S_n$, where f = the frequency of each native species in the species by plot matrix.

Statistical analysis

To assess vegetation change within the dry-mesic and mesic Santa Fe Prairie sites, we used a one-way ANOVA to test for significant differences in $\bar{x}R_n$, $\bar{x}C$ and $\bar{x}C_w$ values among the 1976, 1998, and 2003 data sets. Weighted C values were log-transformed for these tests to achieve normality. Comparisons of the NRI and FQI, as well as S_n and AI, are by inspection at the within-site level of analysis because they represent single values with no mean or variance. As found by Cohen et al. (2004), weighted $\bar{x}C$ values were no more sensitive to temporal change than un-weighted values in our within-site comparison. Weighted and un-weighted C values were also significantly correlated (dry-mesic $r = 0.769$, $P < 0.001$; mesic $r = 0.813$, $P < 0.001$). As a result, only un-weighted values were used for further analysis.

For among-site comparisons, we first tested whether $\bar{x}C$, $\bar{x}R_n$ or S_n values differed across a dry, dry-mesic, mesic, and wet-mesic moisture gradient represented by the data set. In these tests, Illinois and Chicago region C values were compared

using ANOVA in a General Linear Model, while $\bar{x}R_n$ and S_n were tested separately using one-way ANOVA. For C values, we assumed that significant variation across the dry, dry-mesic, mesic, and wet-mesic moisture gradient would represent a bias in assigning coefficients, especially if rare vegetation types, such as dry prairies, had greater mean values. We expected that species richness would peak at a midpoint across the moisture gradient (Curtis 1959). Because Chicago region and Illinois C values did not differ in their within-site comparisons, nor in their moisture gradient patterns, only Chicago region values were used in subsequent tests. To assess the potential stability of the FQI and NRI formulae, we tested for significant correlations between $\bar{x}C$ and S_n , and between $\bar{x}R$ and S_n . We assumed that negative correlations indicated independence between these pairs of variables, which could confound statistical interpretation of either FQI or NRI.

To test and compare NRI and FQI sensitivity to differences among sites over time, we used Repeated Measures Analysis of Variance in a General Linear Model with S_n , $\bar{x}R_n$, NRI, $\bar{x}C$, FQI and W/G as performance variables. Factors in this analysis were INAI quality ($n = 16$ grade A vs. $n = 17$ grade B) and two moisture level categories ($n = 13$ dry/dry-mesic vs. $n = 20$ mesic/wet-mesic). We also used linear regression to analyze the dependence of temporal change in NRI and FQI statistics, as well as the W/G ratio, upon fire frequency. To make these calculations, the temporal change in each variable (e.g., $\Delta_T \bar{x}R_n = \bar{x}R_{n2001} - \bar{x}R_{n1976}$ for each site) was regressed against the frequency of management fires applied to that site.

RESULTS

Within-site comparisons

Species richness and floristic quality statistics

In dry-mesic habitat at Santa Fe Prairie, $\bar{x}R_n$ declined significantly between 1976 and 1998 (Table 1). Although S_n did not

change, the NRI decreased due to the decrease in $\bar{x}R_n$. The AI did not change substantially during this period. By 2003, $\bar{x}R_n$ had increased significantly above original levels, while S_n , NRI, and AI also increased. In mesic prairie at Santa Fe, $\bar{x}R_n$ also declined significantly between 1976 and 1998, with corresponding decreases for S_n and NRI values (Table 1). The AI also dropped during this period. By 2003, species richness in mesic prairie had returned to original levels, while S_n declined slightly and NRI increased. However, the AI increased almost sixfold during this period. In contrast to significant temporal changes in species richness, measures of conservatism were temporally stable. Illinois C values did not differ significantly over the 1976-1998-2003 period for dry-mesic (weighted $P = 0.092$; un-weighted $P = 0.081$) or for mesic (weighted $P = 0.220$; un-weighted $P = 0.090$) habitats. Likewise, neither weighted nor un-weighted Chicago-region C values changed significantly over time for dry-mesic or for mesic prairie (Table 1). The non significant changes in $\bar{x}C$ values, as well as changes in S_n , also resulted in declines for FQI between 1976 and 1998, followed by increases in this index between 1998 and 2003.

Independent measures

In dry-mesic plots at Santa Fe Prairie, vegetation underwent a large compositional shift between 1976 and 1998, with suites of increasing, decreasing, and stable species groups. This shift was associated with a decline in relative abundance of dominant grasses (e.g., *Stipa spartea*, *Sporobolus heterolepis* and *Panicum oligosanthos*) and an increase in sedge abundance (Figure 1), which corresponded to a doubling of the W/G ratio (Table 1). Other declining species included the forbs *Echinacea pallida*, *Coreopsis palmata* and *Aster azureus*, and the native prairie shrub *Amorpha canescens*. Species that appeared in 1998 at comparatively high frequencies included the native forbs *Solidago altissima*, *Commandra umbellata*, *Helianthus grosseratus* and the alien buckthorn. By 2003, there was very little change in the abundance of grasses or sedges, although woody vegetation declined (Figure 2), causing a drop in the

Table 1. Mean (+ SE) variation over time for total native richness (Sn), average plot species richness ($\bar{x}Rn$), Native Richness Index (NRI), alien index (AI), woody/graminoid ratio (W/G), Floristic Quality Index (FQI), average coefficient of conservatism ($\bar{x}C$), and weighted average coefficient of conservatism ($\bar{x}Cw$) in dry-mesic and mesic prairie at the Santa Fe Prairie. Probabilities represent one-way ANOVA for each variable. Similar lower case letters indicate similar means with Newman-Keuls multiple comparisons. FQI is calculated with unweighted C values.

Dry-mesic	1976	1998	2003	Probability
Sn	45	45	49	
$\bar{x}Rn$	9.35 (+.34)a	7.33 (+.52)b	11.55 (+.68)c	P < 0.001
NRI	35.59	27.92	44.95	
AI	2.93	2.82	4.71	
W/G ratio	0.34	0.69	0.49	
$\bar{x}C$	5.45 (+.46)	4.26 (+.38)	4.87 (+.39)	P = 0.144
$\bar{x}Cw$	1.25 (+.26)	0.78 (+.21)	1.14 (+.22)	P = 0.114
FQI	36.56	28.58	34.09	
Mesic	1976	1998	2003	Probability
Sn	60	50	47	
$\bar{x}Rn$	12.75 (+.40)a	9.42 (+.47)b	12.95 (+.57)a	P < 0.001
NRI	52.2	36.84	49.85	
AI	1.65	0.68	4.61	
W/G ratio	0.17	0.68	0.25	
$\bar{x}C$	5.36 (+.39)	4.18 (+.41)	4.43 (+.46)	P = 0.096
$\bar{x}Cw$	1.27 (+.17)	0.84 (+.21)	1.35 (+.26)	P = 0.251
FQI	41.52	29.56	30.37	

W/G ratio (Table 1). However, there was little recovery of formerly dominant grass or forb species and little change in the abundance of native or alien species that appeared in 1998.

Mesic prairie vegetation also underwent a large compositional shift between 1976 and 1998. This shift was also associated with a decline in relative abundance of native grass species (e.g., *Sorghastrum nutans*, *Sporobolus heterolepis* and *Andropogon scoparius*) and increasing abundance of sedges, as well as woody vegetation (Figure 2), which corresponded to a more than threefold increase in the W/G ratio (Table 1). Among forbs, the formerly abundant *Solidago riddellii*, *Allium cernuum*, and *Aster azureus* were not resampled, while increasing forbs included *Solidago altissima*, *S. graminifolia* var. *nuttallii* and *Helianthus grosseserratus*. The native

shrub *Cornus racemosa* and the alien shrub *Rhamnus cathartica* also increased. By 2003, the relative abundance of grasses almost doubled, due to an increase in *Panicum implicatum*, but still remained lower than in 1976, while abundance of sedges increased slightly (Figure 2). Although the W/G ratio returned to near its 1976 value, there was essentially no recovery of formerly dominant grass or forb species, and a slight decline in the abundance of *Carex tetanica* and *Rhamnus* species.

Among-site comparisons

When compared across a landscape moisture gradient, mean $\bar{x}Rn$ and Sn values had similar patterns and were significantly lower for dry habitats, tending toward an expected unimodal peak in mesic habitats (Figure 2). The distribution patterns of Il-

linois and Chicago region mean $\bar{x}C$ values were also similar but significantly lower for Illinois values, and with both measures significantly biased toward higher values for dry prairie habitats (Figure 2). A significant positive correlation occurred between $\bar{x}Rn$ and Sn values (Figure 3), indicating that these values would not operate independently and confound interpretation of NRI. In contrast, $\bar{x}C$ and Sn values were significantly negatively correlated (Figure 3), indicating that they may operate independently and confound interpretation of FQI.

Most measures of species richness varied significantly in relation to INAI quality and moisture gradient, with no significant interactions (Figure 4). Mean $\bar{x}Rn$ and NRI were greater for grade A than for grade B sites, while Sn, $\bar{x}Rn$, and NRI were also higher for mesic/wet-mesic prairies than for dry/dry-mesic prairies. Floristic quality indices were less sensitive to these factors and presented conflicting results because of the negative correlation between $\bar{x}C$ and Sn. Mean values for $\bar{x}C$ did not vary with INAI grade, but were significantly higher for dry/dry-mesic sites due to the bias toward dry prairies. In contrast, FQI values were higher for grade A and for mesic/wet-mesic sites, due to the effect of Sn in the FQI formula. The W/G ratio did differ significantly by quality or habitat. Many of these measures also changed significantly ($P < 0.05$) over time, with increases in Sn, NRI, and the W/G ratio, and a decrease in mean $\bar{x}C$ values.

Linear regressions of temporal change against fire frequency were significant and positive for $\bar{x}Rn$ and negative for the W/G ratio (Figure 5), indicating a positive effect of fire on both species richness and vegetation structure. However, there was no significant relationship between temporal change in $\bar{x}C$ and fire frequency (Figure 5). There was also a significant positive relationship between fire frequency and temporal change in Sn ($r^2 = 0.19$, $P = 0.011$), as well as between fire frequency and both NRI ($r^2 = 0.307$, $P < 0.001$) and FQI ($r^2 = 0.172$, $P = 0.0165$) due to the influence of Sn on these indices. Temporal change in the W/G ratio had a significant negative relationship to temporal change

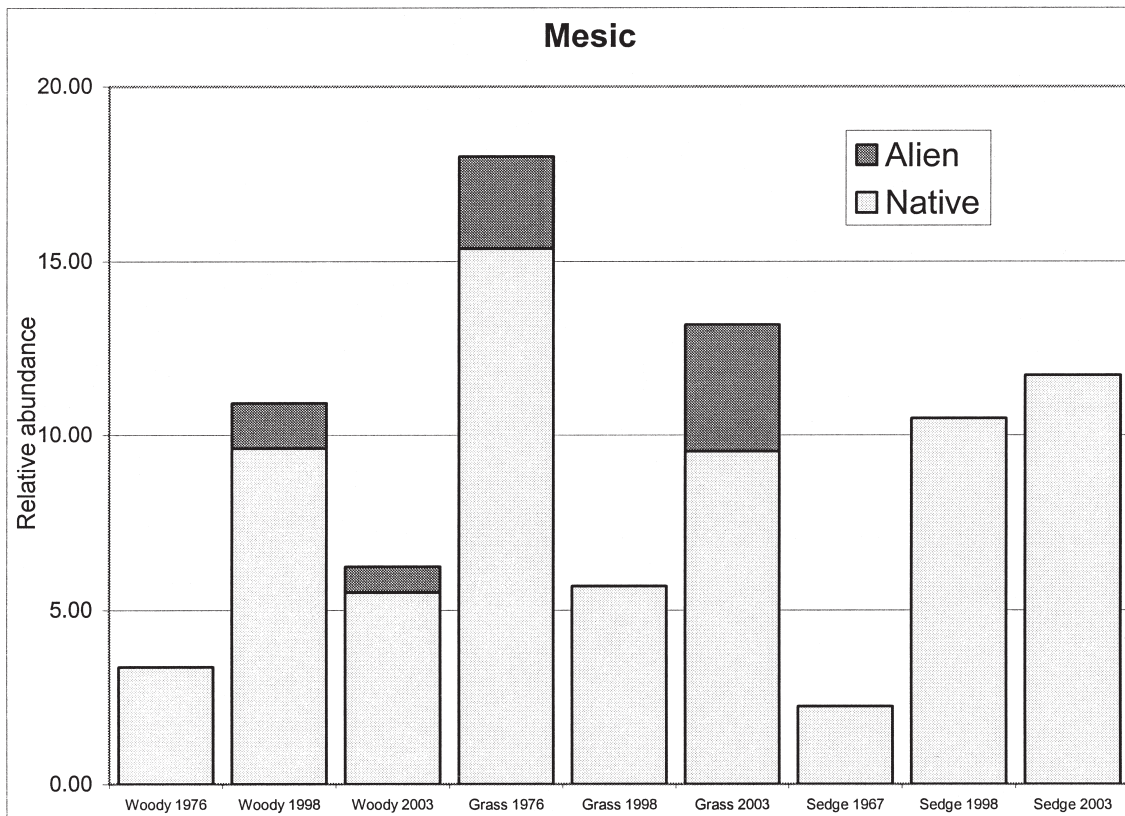
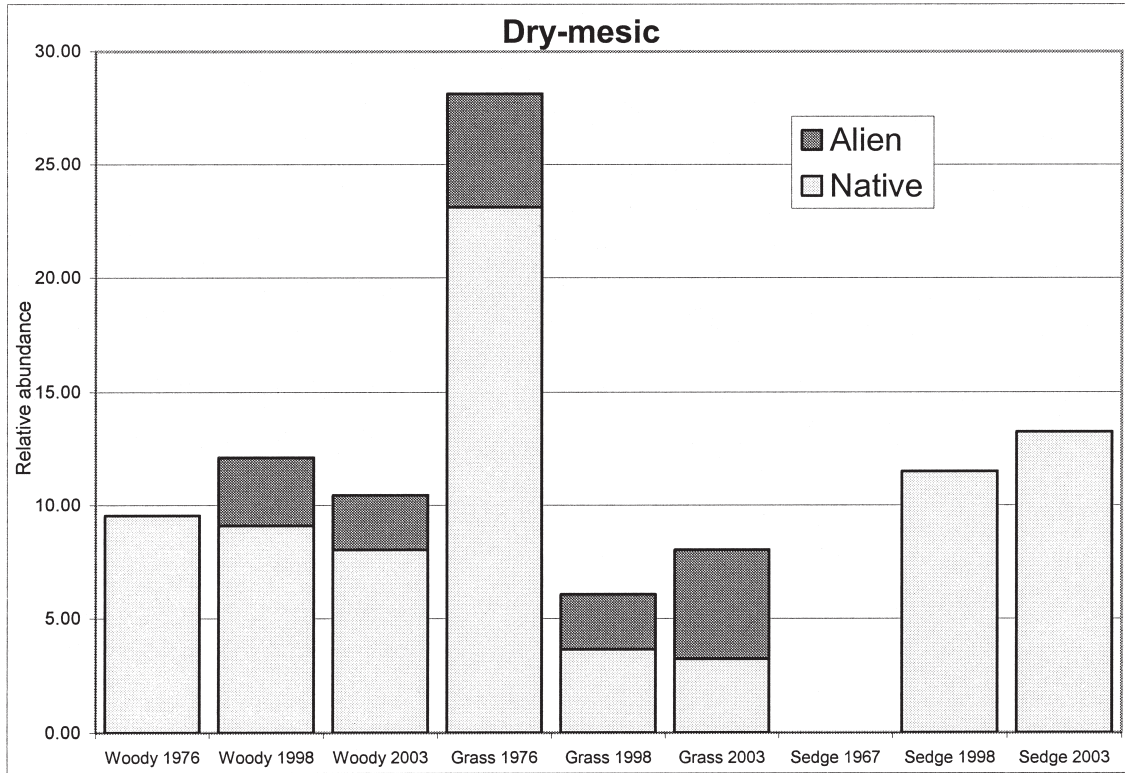
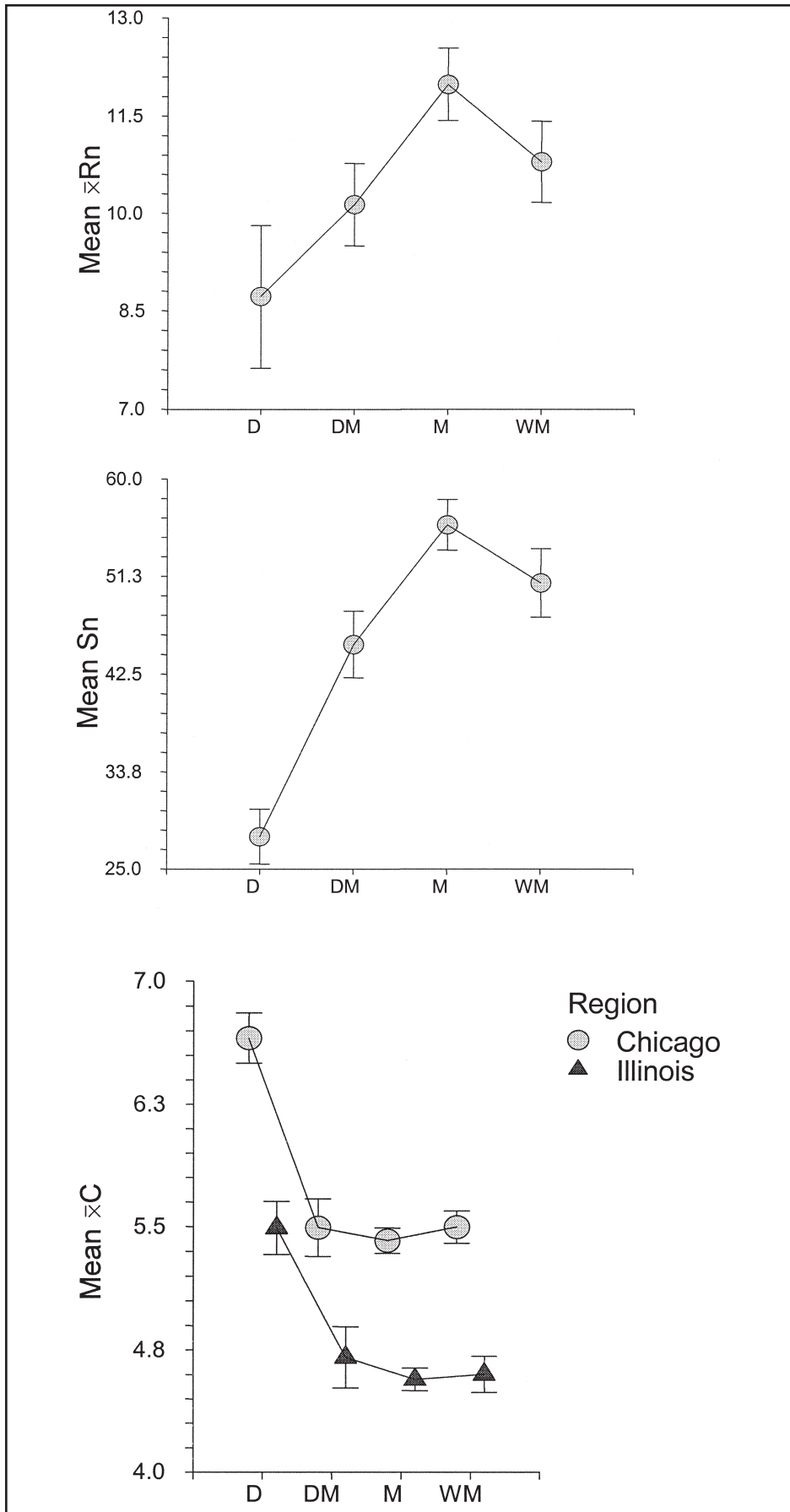


Figure 1. Temporal change in relative abundance of native and alien woody, grass and sedge species in dry-mesic and mesic gravel prairie vegetation at Santa Fe Prairie.



in both $\bar{x}Rn$ ($r^2 = 0.2645$, $P = 0.002$) and $\bar{x}C$ ($r^2 = 0.345$, $P < 0.001$), indicating sensitivity to change in structure for both metrics.

DISCUSSION

Efficacy of species richness

Our results demonstrate that objective measures of species richness can be unambiguous and informative, often more so than complex indices (Hurlbert 1971, Peet 1974, Green 1979). These metrics were also useful at multiple scales of sample size and for comparisons within and among sites. Within sites, the small scale measures of average plot species richness ($\bar{x}Rn$) were most applicable because multiple plot sampling generates a testable mean and variance. At the Santa Fe Prairie, the significant decline in $\bar{x}Rn$ corresponded to deterioration of unburned prairie vegetation through loss of species that contributed to altered composition and structure. For multiple comparisons among sites, testable statistics can be generated for all components of NRI. The sensitivity of NRI, as well as its small ($\bar{x}Rn$) and larger scale (Sn) components, to a priori assignments of INAI grades suggests this index may be a robust indicator of quality, as perceived by the INAI. Nevertheless, application of species richness as a strict measure of qualitative change can be problematic. This is shown by the significant increase in $\bar{x}Rn$ to 1976 levels at Santa Fe Prairie even though compositional recovery had not occurred.

The positive correlations of species richness metrics with fire frequencies and the negative correlation of $\bar{x}Rn$ with the W/G ratio indicate strong agreement with factors that regulate quality. This linkage occurs

Figure 2. Mean (\pm SE) variation across a moisture gradient for Illinois and Chicago region average Coefficients of Conservatism ($\bar{x}C$), average native plot species richness ($\bar{x}Rn$) and total native richness (Sn). D = dry, DM = dry-mesic, M = mesic, WM = wet-mesic. ANOVA: $\bar{x}C$ (Illinois vs Chicago $P < 0.001$, moisture gradient $P < 0.001$, Illinois x Chicago $P = 0.558$), $\bar{x}Rn$ ($P = 0.04$), Sn ($P < 0.001$). C values based on Swink & Wilhelm (1994).

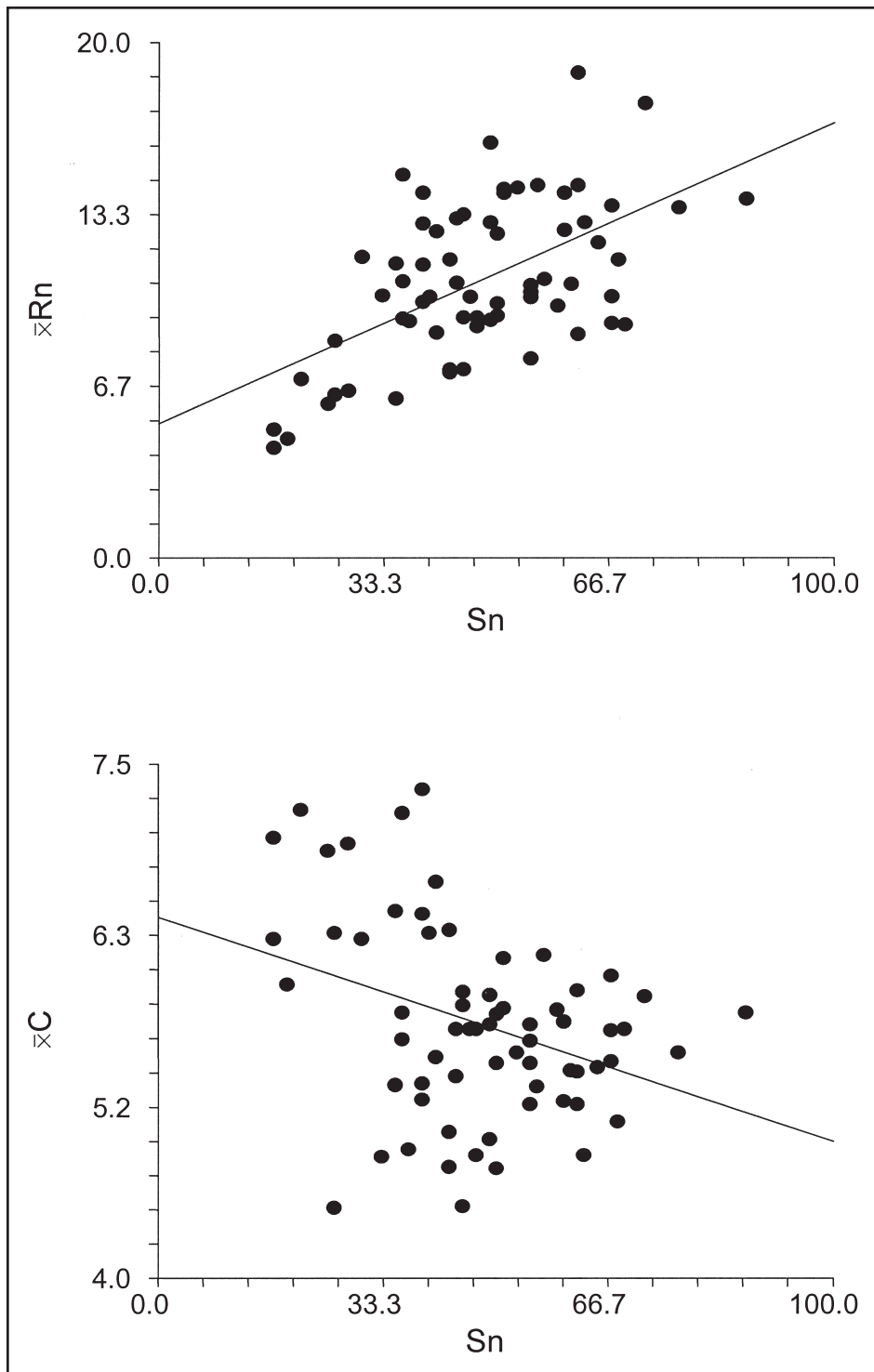


Figure 3. Correlations between average Coefficient of Conservatism ($\bar{x}C$) and total native richness (S_n) ($r = -0.152$, $P = 0.005$), and between average plot species richness ($\bar{x}R_n$) and total native richness (S_n) ($r = 0.567$, $P < 0.001$). C values based on Swink & Wilhelm (1994).

because fire reduces woody vegetation while maintaining grass cover and prairie species richness (Collins and Glenn 1988, Collins and Gibson 1990). As a result, fire also tends to stabilize high quality prairie

vegetation (Bowles and Jones 2004). In turn, fire exclusion allows accumulation of woody vegetation and grass litter that reduces small-scale native richness (Kucera and Koelling 1964, Collins 1987, Gibson

and Hulbert 1987, Collins and Gibson 1990). Declining plants in unburned prairie also tend to represent fire-dependent late-successional species, while increasing species include rhizomatous generalists (such as *Solidago altissima* and *Helianthus grosseserratus*) or woody invaders that can persist without fire or increase under artificial disturbance regimes (e.g., Bowles et al. 2002, Bowles and Jones 2004). Because prairie plants that decline with fire suppression are also often small statured (Leach and Givnish 1996), species richness probably also declines as larger generalist species increase in abundance.

Efficacy of Floristic Quality

In contrast to NRI statistics, the much lower effectiveness of FQI and $\bar{x}C$ values in detecting negative changes in composition and structure, as well as responses to fire, indicates that these statistics are problematic as measures of quality, as well as for detecting change in quality in response to management. The inability of $\bar{x}C$ values to distinguish temporal change in composition and structure at Santa Fe Prairie, and to differentiate between INAI quality grades, can have multiple interpretations; we consider the two most apparent. One is that the C values were correct, and that the Santa Fe Prairie did not change in quality, and that the a priori INAI grades were not correct. This conclusion is not supported by independent data, which indicated the Santa Fe Prairie was clearly in an advanced state of deterioration by 1998 (Bowles et al. 1998). Likewise, the INAI grade A and B assignments reflect differences in vegetation composition, as well as different responses to fire, which stabilizes grade A vegetation and drives successional change in Grade B vegetation (Bowles and Jones 2004).

A more likely conclusion about the conflicts between NRI and FQI is that the subjectively assigned C values are not precise measures of conservatism and are biased toward rare species or by personal preference. Nevertheless, the significant relationship between change in C values and in the W/G ratio supports an argument that these values are logical. However, us-

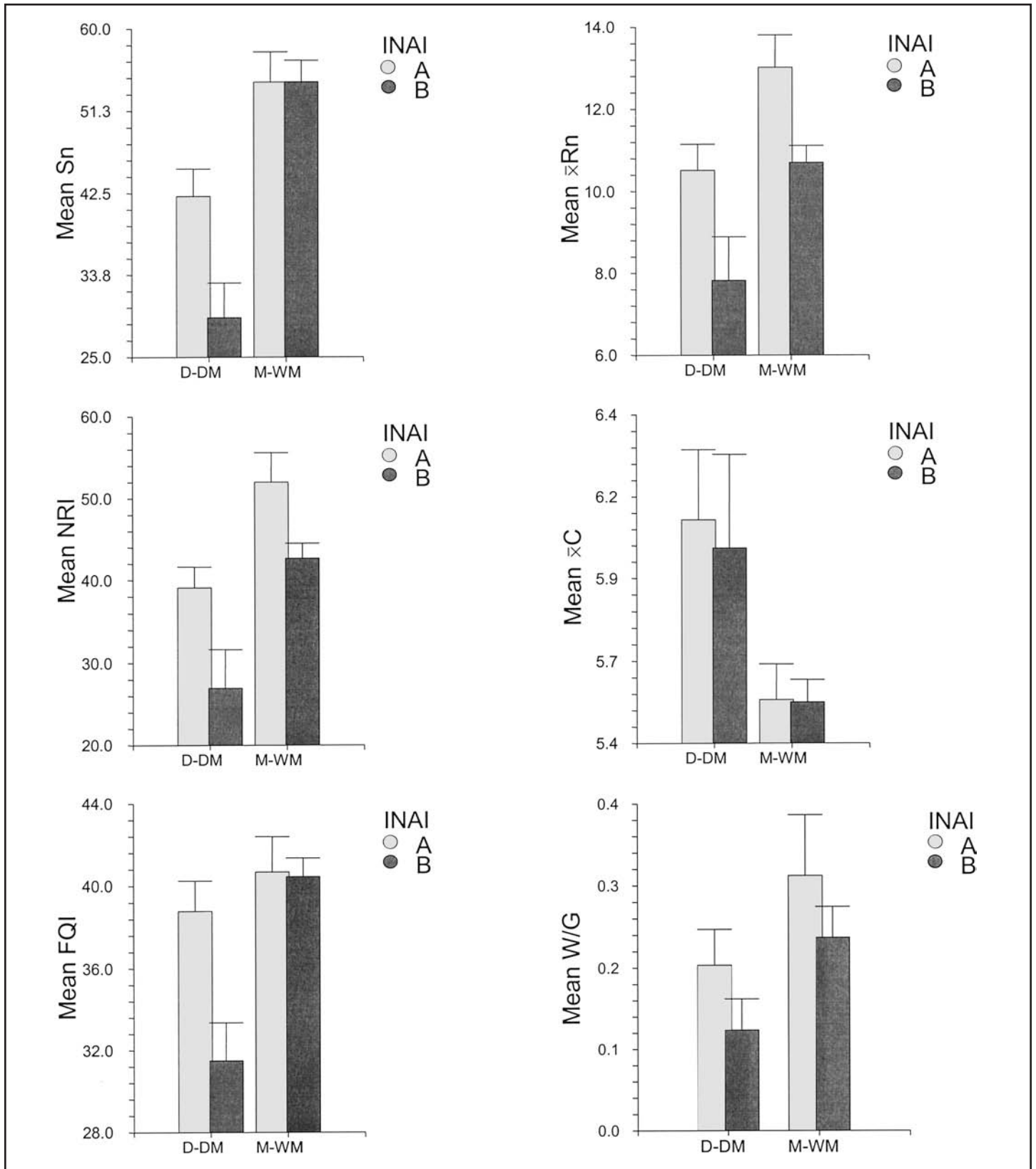
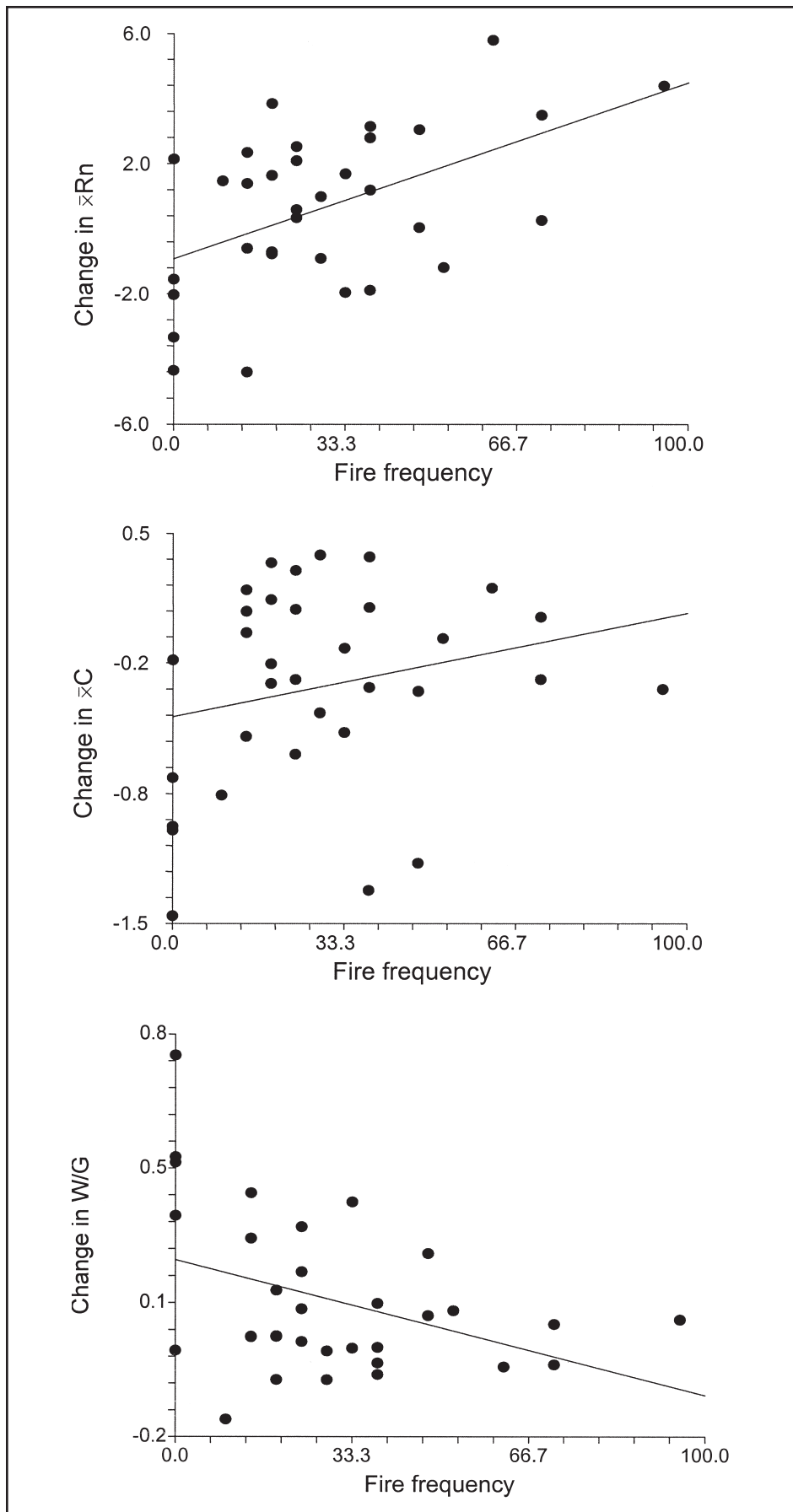


Figure 4. Mean (\pm SE) variation in native species richness (Sn), average native plot species richness ($\bar{x}Rn$), Native Richness Index (NRI), average Coefficient of Conservatism ($\bar{x}C$), Floristic Quality Index (FQI) and woody/graminoid ratio(W/G) in relation to INAI quality grade and moisture gradient. ANOVA probabilities: Sn (INAI quality = 0.114, moisture gradient < 0.001), $\bar{x}Rn$ (INAI quality = 0.009, moisture gradient = 0.005), NRI (INAI quality = 0.010, moisture gradient < 0.001), $\bar{x}C$ (INAI quality = 0.821, moisture gradient = 0.02), FQI (INAI quality = 0.057, moisture gradient = 0.008), W/G ratio (INAI quality = 0.230, moisture gradient = 0.089). All moisture gradient * INAI quality interactions > 0.05. C values based on Swink & Wilhelm (1994).



ing C values to measure quality represents a tautology that does not support statistical testing if quality is perceived based on presence of plants that receive high C values. Reassigning C values to represent higher numbers for declining species or lower numbers for increasing species at Santa Fe Prairie could give results that correspond to the actual changes in these sites. However, because multiple combinations of altered C values would achieve similar results, there is a lack of precise knowledge about which values would be “correct.” Moreover, adjusting C values to compensate for lack of precision is also tautological if adjusted values are then used to test perceived changes in quality. The greater mean $\bar{x}C$ values for dry prairies more likely occurs because their habitats are uncommon landscape features in northeastern Illinois (Willman 1971) than because they rank higher in quality than natural areas in more mesic habitats. This bias toward rare species would confound interpretation of cause and effect statistical tests because it would be unknown whether differences in mean C values reflect differences in quality or different abundances of rare species.

FQI is more effective than C values alone in differentiating between quality and temporal change because FQI functions as a weighted species richness index due to its incorporation of S_n in its formula. However, the accuracy of this measure is weakened due to bias and lack of precision in C values, and because these subjective values may operate independently from species richness. Although Rooney and Rogers (2002) and Cohen et al. (2004) suggested using only C values to avoid this problem, our data suggest that the absence of weighting for species richness makes the statistic less reliable. For example, in a study comparing natural prairie remnants with a restoration, Allison (2002) found higher $\bar{x}C$ values for the restoration. This

Figure 5. Relationships between fire frequency and temporal change in average native plot species richness ($\bar{x}Rn$) ($r^2 = 0.252$, $P = 0.0039$), average Coefficient of Conservatism ($\bar{x}C$) ($r^2 = 0.056$, $P = 0.184$), and the ratio of woody to graminoid species (W/G ratio) ($r^2 = 0.151$, $P = 0.0255$). C values based on Swink & Wilhelm (1994).

paradox might result from improperly assigned C values, focus on restoring species with higher C values, or sampling bias. However, Allison also found higher species richness for natural prairies, which seems consistent with our results.

CONCLUSIONS

The SRI, or NRI, and FQI function as weighted species richness indices because their mathematical formulae include S_n , a true measure of species richness. The NRI integrates S_n with $\bar{x}R_n$, which is a small scale measure of native species richness, or species density, into a multiplicative index in which sensitivity is based on positively correlated metrics. The FQI differs by incorporating independent, and potentially negatively correlated qualitative and quantitative measures into a multiplicative index. Because S_n is dependent upon the species-area relationship (Hurlbert 1971, Rosenzweig 1995), both NRI and FQI are sensitive to sample size and to the scale of plot dispersion – larger plots, more plots, or more widely dispersed plots increase S_n . Although the species-area effect on these indices is damped by using either $\ln S_n$ in NRI or by $\sqrt{S_n}$ in FQI, both require identical sample scale when used to compare sites or treatments. However, $\bar{x}R_n$ and $\bar{x}C$ have radically different effects on their respective indices. Plot species richness usually stabilizes above a threshold sample size (Elzinga et al. 1998) and provides a precise testable metric. Despite this precision, application of NRI as a strict measure of quality is problematic without supportive information. Species richness or density also may be higher at intermediate levels of natural disturbance (Connell 1978) or at intermediate positions along gradients of biomass and environmental stress (Grime 1979), and may increase with increasing canopy openness in savanna and forest (Bowles and McBride 1998, Bowles et al. 2000). As a result, NRI values should be most useful in ranking different sites within, but not among, vegetation types. Coefficient of Conservatism values could fare worse if bias, lack of precision, and tautological application confound theoretical testing and interpretation. Nevertheless, the FQI concept remains intuitively attrac-

tive because it attaches qualitative metrics to plant communities that often require ranking for preservation, management, and restoration. However, when used independently, FQI or average C values have potential to provide false information that could affect management or preservation actions. They may be most applicable in making comparisons between extremely low vs. high quality vegetation, such as early vs. late-successional prairies (e.g., Taft et al. in press). FQI also may have value in expressing qualitative differences to lay audiences when alternative unbiased measures support its use.

ACKNOWLEDGMENTS

We thank the Illinois Nature Preserves Commission, the Illinois Department of Natural Resources, the Forest Preserve Districts of DuPage, Cook, Kane, Lake, McHenry and Will counties, Lake Forest Open Lands, Downers Grove Park District, Illinois-Michigan Canal National Heritage Corridor Civic Center Authority, and many private landowners for permission to collect data or for providing management information. We also thank the Illinois DNR, as well as the original INAI staff, for historic data, and Deborah Antlitz, Steve Byers, Maggie Cole, Stan Johnson, Dan Kirk, Don McFall, Kelly Neal, Deb Nelson, Steve Packard, Brad Semel, Joe Roth, John White, John and Jane Balaban, Ken Klick, Marcy DeMauro, Drew Ullberg for logistic support. Tim Bell, Christopher Dunn, Jenny McBride, Noel Pavlovic, Bill Sluis, Amy Symstad, Chris Whelan, and two anonymous reviewers provided extremely helpful reviews, discussion or statistical advice. This work received funding support from the Illinois Department of Natural Resources, Chicago District of the U.S. Army Corps of Engineers, CorLands, Chicago Wilderness, Illinois Conservation Foundation, USDA Forest Service, and U.S. Fish and Wildlife Service.

Marlin Bowles is a Plant Conservation Biologist at The Morton Arboretum. His interests include long-term monitoring of plant communities and rare plant populations, and the restoration ecology of rare plants.

Michael Jones is a Botanist with Christopher B. Burke Engineering, Ltd. His interests also include long-term monitoring of plant communities, as well as assessing the status of endangered plant populations. Both authors have been studying the vegetation of the Chicago region for the last 20 years.

LITERATURE CITED

- Allison, S.K. 2002. When is a restoration successful? Results from a 45-year-old tallgrass prairie restoration. *Ecological Restoration* 20:10-17.
- Bowles, M.L., and J. McBride 1998. Vegetation composition, structure, chronological change in a decadent midwestern North American savanna remnant. *Natural Areas Journal* 18:14-27.
- Bowles, M., and M. Jones. 2004. Long term changes in Chicago region prairie vegetation in relation to fire management. *Chicago Wilderness Journal* 2:7-15. Available online <[http://www.chicagowilderness.org/members/cwjournal/](http://www.chicagowilderness.org/members/cwjjournal/)>.
- Bowles, M., M. Jones, J. McBride, T. Bell, and C. Dunn. 2000. Structural composition and species richness indices for upland forests of the Chicago region. *Erigenia* 18:30-57.
- Bowles, M., M. Jones, and J.L. McBride. 2002. Twenty-year changes in burned and unburned sand prairie remnants in northwestern Illinois and implications for management. *American Midland Naturalist* 149:35-45.
- Bowles, M., J. McBride, R. Hyerczyk, M. Jones, R.F. Betz, and S. Johnson. 1998. Santa Fe Prairie Master Plan. Prepared by The Morton Arboretum for the Illinois Nature Preserves Commission, Lisle, Ill.
- Cohen, M.J., S. Carstenn, and C.R. Lane. 2004. Floristic quality indices for biotic assessment of depressional marsh condition in Florida. *Ecological Applications* 14:784-794.
- Collins, S.L. 1987. Interactions of disturbances in tallgrass prairie: a field experiment. *Ecology* 68:1243-1250.
- Collins, S.L., and D.J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. Pp. 81-98 in S.L. Collins and L.L. Wallace, eds., *Fire in Tallgrass Prairie Ecosystems*, University of Oklahoma Press, Norman.
- Collins, S.L., and S.M. Glenn. 1988. Disturbance and community structure in North American prairies. Pp. 131-143 in H.J. During, M.J.A. Werger, and J.H. Willems, eds., *Diversity and Pattern in Plant Com-*

- munities. Academic Publishing, The Hague, The Netherlands.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1309.
- Cowles, H.C. 1901. The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification for plant societies. *Botanical Gazette* 31:73-108, 145-182.
- Curtis, J.T. 1959. *The Vegetation of Wisconsin*. University of Wisconsin Press, Madison.
- Curtis, J.T., and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476-496.
- Elzinga, C.L., D.W. Salzer, and J. Willoughby. 1998. *Measuring and Monitoring Plant Populations*. BLM Technical Reference 1730-1. U.S. Bureau of Land Management, Denver, Colo.
- Francis, C.M., J.J.W. Austen, J.M. Bowles, and B. Draper. 2000. Assessing floristic quality in southern Ontario woodlands. *Natural Areas Journal* 20:66-77.
- Green, R.H. 1979. *Sampling design and statistical methods for environmental biologists*. J. Wiley, New York.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. J. Wiley, New York.
- Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:172-185.
- Herman, K.D., L.A. Masters, M.R. Penskar, A.A. Reznicek, G.S. Wilhelm, and W.W. Brodowicz. 1997. Floristic quality assessment: development and application in the state of Michigan (USA). *Natural Areas Journal* 17:256-279.
- Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52:577-586.
- Kilburn, P.D. 1959. The prairie-forest ecotone in northeastern Illinois. *American Midland Naturalist* 62:206-217.
- Kirt, R.R. 1997. A nine-year assessment of successional trends in prairie plantings using seed broadcast and seedling transplant methods. Pp. 144-153 in C. Warwick, ed., *Proceedings of the Fifteenth North American Prairie Conference*, October 23-26, 1996. Natural Areas Association, St. Charles, Ill.
- Kucera, C.L., and M. Koelling. 1964. The influence of fire on composition of central Missouri prairies. *American Midland Naturalist* 72:142-147.
- Leach, M., and T. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273:1555-1558.
- Lopez, R.D., and M. Siobhan Fennessy. 2002. Testing the floristic quality assessment index as an indicator of wetland condition. *Ecological Applications* 12:487-497.
- Magurran, A.E. 1988. *Ecological Diversity and its measurement*. Princeton University Press, Princeton, N.J.
- Matthews, J.W. 2003. Assessment of the floristic quality index for use in Illinois, USA, wetlands. *Natural Areas Journal* 23:53-60.
- Moran, R.C. 1978. Presettlement vegetation of Lake County, Illinois. Pp. 12-18 in D.C. Glenn-Lewin and R.Q. Landers, eds., *Proceedings of the Fifth Midwest Prairie Conference*, August 22-24, 1976, Iowa State University, Ames.
- Peet, R.K. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics* 5:285-307.
- Rooney, T.P., and D.A. Rogers. 2002. The modified floristic quality index. *Natural Areas Journal* 22:340-344.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, U.K.
- Swink, F., and G. Wilhelm. 1994. *Plants of the Chicago region*. Indiana Academy of Science, Indianapolis.
- Taft, J.B., G.S. Wilhelm, D.M. Ladd and L.A. Masters. 1997. Floristic quality assessment for vegetation in Illinois: a method for assessing vegetation integrity. *Eriogenia* 15:3-95.
- Taft, J.B., C. Hauser, and K.R. Robertson. In press. Comparison of indices for estimating floristic integrity in tallgrass prairie. *Biological Conservation*.
- Werner, K.J., and J.B. Zedler. 2002. How sedge meadows, microtopography, and vegetation respond to edimentation. *Wetlands* 22:451-466.
- White, J. 1978. *Illinois natural areas inventory technical report*. Department of Landscape Architecture, University of Illinois, Urbana-Champaign, and Natural Land Institute, Rockford, Ill.
- White, J., and M. Madany. 1981. Classification of prairie communities. Pp. 169-171 in: R.L. Stuckey and K.J. Reese, eds., *The Prairie Peninsula--in the "Shadow" of Transeau: Proceedings of the Sixth North American Prairie Conference*, August 12-17, 1978. Ohio Biological Survey Notes No. 15, Columbus.
- Wilhelm, G.S., and D. Ladd. 1988. Natural areas assessment in the Chicago region. Pp. 361-375 in *Transactions of the 53rd North American Wildlife and Natural Resources Conference*, March 18-23, 1998 in Louisville, Kentucky. Wildlife Management Institute, Washington, D.C.
- Willman, H.B. 1971. *Summary of the geology of the Chicago area*. Circular 460, Illinois State Geological Survey, Urbana.

APPENDIX I

See pp. 28-29.

APPENDIX II

See pp. 29-30.

APPENDIX I

Change in frequencies of species (excluding forbs with < 20% frequency) sampled in dry-mesic gravel prairie at the Santa Fe Prairie. Species ranked by frequencies in 1976, or later if initially absent. Nomenclature follows Swink & Wilhelm (1994), A = alien, F= Forb, G = graminoid, W= woody.

Habit	Species	1976	1998	2003
AF	<i>Achillea millefolium</i>	5.00	4.76	
AF	<i>Daucus carota</i>	5.00		
AF	<i>Dispacus slyvestris</i>		4.76	
AG	<i>Poa compressa</i>	50.00	14.29	
AG	<i>Poa pratensis</i>		4.76	25.00
AG	<i>Agrostis alba</i>			25.00
AG	<i>Phalarus anundinacea</i>			10.00
AW	<i>Rhamnus cathartica</i>		23.81	25.00
AW	<i>Rhamnus frangula</i>			5.00
F	<i>Echinacea pallida</i>	85.00		
F	<i>Smilacina stellata</i>	75.00	76.19	100.00
F	<i>Monarda fistulosa</i>	50.00	19.05	45.00
F	<i>Cirsium discolor</i>	35.00		5.00
F	<i>Euphorbia corrolata</i>	30.00	28.57	30.00
F	<i>Coreopsis palmata</i>	30.00		5.00
F	<i>Phlox pilosa</i>	30.00		
F	<i>Convolvulus sepium</i>	25.00	38.10	25.00
F	<i>Aster azureus</i>	25.00		
F	<i>Solidago gigantea</i>	15.00	14.29	45.00
F	<i>Coreopsis tripteris</i>	15.00	4.76	50.00
F	<i>Silphium integrifolium</i>	15.00		35.00
F	<i>Hypericum sphaerocarpum</i>	10.00	9.52	70.00
F	<i>Solidago canadensis</i>		76.19	60.00
F	<i>Commandra umbellata</i>		23.81	40.00
F	<i>Galium boreale</i>		23.81	35.00
F	<i>Heliantus grossesseratus</i>		23.81	45.00
F	<i>Oenother pilosella</i>		19.05	5.00
F	<i>Solidago graminifolia var. nuttallii</i>		14.29	20.00
F	<i>Thalictrum dasycarpum var. hypoglaucum</i>		14.29	50.00
F	<i>Aster simplex</i>			20.00
G	<i>Stipa spartea</i>	95.00		5.00
G	<i>Sporobolus heterolepis</i>	55.00		10.00
G	<i>Panicum oligosanthos var. scribnerianum</i>	50.00		
G	<i>Sorghastrum nutans</i>	25.00		5.00
G	<i>Andropogon gerardii</i>	5.00		
G	<i>Carex tetanica</i>		85.71	85.00

continued

APPENDIX I – CONTINUED

Habit	Species	1976	1998	2003
<i>continued</i>				
G	<i>Panicum implicatum</i>		9.52	20.00
G	<i>Calamagrosis canadensis</i>		4.76	45.00
G	<i>Eleocharis compressa</i>		4.76	15.00
G	<i>Carex pellita</i>			20.00
W	<i>Amorpha canescens</i>	40.00		5.00
W	<i>Rosa sp.</i>	25.00	42.86	70.00
W	<i>Salix humulis</i>	20.00		
W	<i>Cornus racemosa</i>	10.00	14.29	20.00
W	<i>Rubus occidentalis</i>		4.76	
W	<i>Vitis riparia</i>		4.76	5.00

APPENDIX II

Change in frequencies of species (excluding forbs with < 20% frequency) sampled in mesic gravel prairie at the Santa Fe Prairie. Species ranked by frequencies in 1976, or later if initially absent. Nomenclature follows Swink & Wilhelm (1984), A = alien, F= Forb, G = graminoid, W= woody.

Habit	Species	1976	1998	2003
AF	<i>Achillea millefolium</i>			5.00
AF	<i>Lepidium campestre</i>			5.00
AG	<i>Poa compressa</i>	35.00		
AG	<i>Agrostis alba</i>			5.00
AG	<i>Poa pratensis</i>			25.00
AG	<i>Phalaris arundinacea</i>			20.00
AW	<i>Rhamnus cathartica</i>		12.50	5.00
AW	<i>Rhamnus frangula</i>			5.00
F	<i>Smilacina stellata</i>	90.00	66.67	85.00
F	<i>Allium cernuum</i>	60.00		
F	<i>Silphium terebinthinaceum</i>	55.00	16.67	
F	<i>Physostegia virginiana</i>	55.00		5.00
F	<i>Solidago riddellii</i>	55.00		
F	<i>Coreopsis tripteris</i>	50.00	8.33	
F	<i>Senecio paupercula</i>	50.00	8.33	
F	<i>Ratibida pinata</i>	45.00	8.33	10.00
F	<i>Aster azureus</i>	45.00		
F	<i>Aster ericoides</i>	45.00		

continued

APPENDIX II – CONTINUED

Habit	Species	1976	1998	2003
	<i>continued</i>			
F	<i>Convolvulus sepeium</i>	35.00	41.67	40.00
F	<i>Fragaria virginiana</i>	35.00	20.83	20.00
F	<i>Satureja arkansanum</i>	30.00		15.00
F	<i>Phlox glaberrima var. interior</i>	30.00		
F	<i>Solidago gigantea</i>	25.00	29.17	25.00
F	<i>Euphorbia corolata</i>	25.00	29.17	10.00
F	<i>Galium obtusum</i>	25.00	12.50	60.00
F	<i>Rudbeckia hirta</i>	25.00		10.00
F	<i>Lysimachia quadriflora</i>	20.00		
F	<i>Hypericum sphaerocarpum</i>	15.00	20.83	95.00
F	<i>Monarda fistulosa</i>	15.00	20.83	15.00
F	<i>Commandra umbellata</i>	5.00	8.33	45.00
F	<i>Solidago altissima</i>		54.17	60.00
F	<i>Thalictrum dasycarpum var. hypoglaucum</i>		54.17	55.00
F	<i>Helianthus grossesseratus</i>		41.67	95.00
F	<i>Solidago graminifolia var. nuttallii</i>		41.67	65.00
F	<i>Lycopus americanus</i>		41.67	35.00
F	<i>Stachys tenuifolia var. hispida</i>		4.17	50.00
F	<i>Gaura biennis</i>			60.00
G	<i>Sporopolus heterolepis</i>	50.00	8.33	15.00
G	<i>Andropogon scoparius</i>	35.00		
G	<i>Caxex tetanica</i>	25.00	91.67	75.00
G	<i>Sorghastrum nutans</i>	55.00	4.17	
G	<i>Panicum implicatum</i>	10.00	33.33	85.00
G	<i>Andropogon gerardii</i>	10.00		15.00
G	<i>Stipa spartea</i>	10.00		
G	<i>Eleocharis compressa</i>		4.17	65.00
W	<i>Rosa sp.</i>	35.00	41.67	60.00
W	<i>Cornus racemosa</i>	5.00	41.67	5.00
W	<i>Amorpha canescens</i>	5.00		
W	<i>Crataegus sp.</i>		8.33	10.00