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Characterization of Central Iowa Forests with Permanent Plots

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We describe a standard methodology for establishing and inventorying the woody vegetation in 0.1-ha permanent forest plots and we utilize the data from 86 plots to characterize the mature forest vegetation of central Iowa. Obvious differences existed between bottomland hardwoods and upland forest stands, but disturbed uplands contained species typical of bottomlands. Little-disturbed upland forest plots included a variety of species associations, but variation among plots was continuous. The trees dominating the mature upland forests of central Iowa grow in a wide variety of habitats, with the result that predictability of stand structure at any location is limited. Stands on northerly and southerly aspects did differ consistently from one another, but other aspects were not intermediate in character. The overall structure of the forest stands we inventoried was typical of old secondary forests. Even the oldest forests of central Iowa are still relatively young, and their structure and composition is likely to change in the coming decades. The permanent plots we established will allow for documentation and analysis of this change.

INDEX DESCRIPTORS: floodplain forest, forest sampling, forest structure, temperate deciduous forest, oak-hickory forest, ordination.

Permanently delineated forest plots can be valuable tools for ecologists, foresters, land managers, and educators. Upon establishment and inventory, permanent plots provide information on the woody structure and floristic composition of individual forests, on variations among forest types, on population attributes of the trees present, and the information necessary to evaluate species-environment relationships. Over the long term, permanent plots provide insights into forest dynamics; changes in tree population attributes; and information on tree growth rates, sizes, and lifespans in contrasting environments. They also may be used to evaluate theories of long-term forest succession in Iowa and to monitor changes in invasive species. Thus, the establishment, monitoring, and evaluation of permanent forest plots can enhance conservation, restoration, and land management efforts.

Since 1983 we have adapted and improved upon a standard permanent forest plot design, and we have established a number of permanent plots in forests in central Iowa. Our objectives in this paper are to describe this methodology and to use the data collected to characterize broadly the principal forest types of central Iowa. Similar efforts in other locations in the state, undertaken with the same methodology, would allow for a rigorous analysis of the forest types of Iowa, their determining factors, their possible successional interrelationships, and the effects of land management activities.

METHODS

We established and inventoried 86 permanent, 0.1-ha plots in central Iowa. Plots were established in Boone (Ledges State Park), Dallas (Silvers-Smith Woods State Preserve), Hardin (Fallen Rock State Preserve, Hardin City Woodland State Preserve, Mann Wilderness Area State Preserve), Polk (Strasser Woods State Preserve), Story (Pammel Woods), Tama (Mericle Woods State Preserve), Warren (Woodland Mounds State Preserve), and Webster (Woodman

Hollow State Preserve) Counties. The 38 plots located in Ledges State Park and were originally inventoried by Johnson-Groh (1985). Our analysis is based on data from these same plots collected in 1994-97. Most of the established plots were within or near the Des Moines Lobe, the most recently glaciated region of Iowa. This region is dominated by soils derived from Wisconsin till (Iowa Agriculture and Home Economics Experiment Station, 1978). Plant nomenclature used herein follows Eilers and Roosa (1994).

Site selection

No forests in Iowa are undisturbed by human activities, but we selected sites in parks and preserves that best exemplify the most mature forests of central Iowa. Specific plot locations were chosen to minimize within-plot environmental heterogeneity and to maximize the likelihood that the vegetation of each plot would reflect a single physical habitat and disturbance history. Multiple plots were established in each forest to allow for comparisons among habitat types and to document local variability. We specifically attempted to locate plots on ridgetops, slopes of different aspects, and in bottomlands in each forest location that we inventoried. Obvious recent disturbances such as newly formed treefall gaps and landslips were avoided. Our objective in site selection was to characterize the mature forest vegetation; alternative objectives would require different site selection protocols.

Permanent plot establishment

Each plot measured 50 m × 20 m, with the long axis being parallel to the prevailing topographic contours (Fig. 1). This plot size and shape has long been used in forest studies (e.g., Whittaker 1956, Glenn-Lewin 1974, 1977, Peet 1978, Rice and Westoby 1983) and therefore enhances the potential for comparisons among forest regions. Screw-style metal tree anchors, widely available in hardware stores, were set into the ground at each corner and at each end of the centerline to permanently mark the specific plot location. The anchors were screwed into the ground until only the large eyelet

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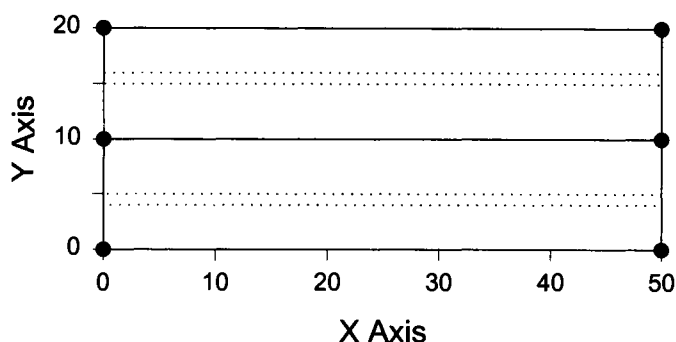


Fig. 1. Permanent forest sample plot design. Solid circles represent iron tree anchors. The long axis is oriented parallel to the slope. All trees and vines ≥ 1.5 m tall within the plot are inventoried, and all individuals > 2.5 cm dbh are mapped by their X-Y coordinates. All woody plants ≥ 20 cm tall but < 1.5 m tall are tallied within the two 1-m wide transects delineated with broken lines.

protruded above the leaf duff. In some locations standard metal fenceposts were placed at each end of the centerline; these made plot relocation faster and easier. However, they are more obtrusive in the natural setting.

One large, healthy hardwood tree near each corner of the plot was tagged with a numbered aluminum tag that was nailed part way into the tree with a long aluminum nail at a height of ~ 2.5 m, facing the corner anchor. The distance from each tagged witness tree to the nearest corner anchor was measured to the nearest 0.1 m, and the compass direction from the tree to the corner anchor was recorded to the nearest 1° . We measured the diameter at breast height (dbh, 1.4 m) and recorded the species of each of the four witness trees. These witness trees provide the best means of relocating the corner anchors, and they are much more useful if they are species uncommon in the area or are of unusual size or shape. A hand-sketched map of each plot and the surrounding area, including foot trails, streams, erosion gullies, ridgetops, etc. was made, and the precise location of each plot was marked on an enlarged photocopy of a topographic sheet.

Plot measurements

Each plot was delineated in the field with metric tapes. A zero corner was defined so that a Cartesian coordinate system could be used for mapping trees (Fig. 1). We designated the 50-m long axis to be the X coordinate and the 20-m axis to be the Y coordinate. Ideally, five 50-m tapes were strung lengthwise across the plot, subdividing it into four $5 \text{ m} \times 50 \text{ m}$ transects, to facilitate inventory. The compass direction of the centerline was recorded. The slope of each plot was determined with a clinometer, with readings taken from the upper side to the lower side at each end and at the center of the long axis ($n=3$). The aspect was determined with a compass and was generally perpendicular to the centerline. Each plot was designated as being in one of the following topographic positions: ridgetop (including level uplands), upper slope, middle slope, lower slope, or bottomland.

Inventory Techniques

We used a three-step process for inventorying the woody plants within each plot, tallying first the trees, then saplings, then small stems. For tallying trees, each plot was subdivided into four parallel $5 \text{ m} \times 50 \text{ m}$ transects. Each living and dead woody plant stem ≥ 8 cm circumference at breast height (cbh, measured at 1.4 m height) within each transect was identified to species, its cbh was measured,

and its location (X and Y coordinates) was recorded. Individual plants frequently had multiple stems and it was not always possible to identify the number of genetically distinct individuals in each plot. All our inventories were based on tallies of stems. If stems arising from the same rootstock were united at a height of 50 cm above the soil level, they were considered to be branches of a single stem. In plot analyses the total basal area of all branches was combined to determine the basal area of the parent stem, and the equivalent diameter of that stem was derived from the total basal area of all branches. If multiple stems arose as basal shoots or root sprouts, and were not joined together 50 cm above the ground, they were tallied as individuals.

Next we tallied all stems > 1.5 m tall but < 8 cm cbh to species, without recording their specific locations within the plot. This was accomplished by passing through each of the 5-m wide transects and tallying species. Within this and smaller size classes it was not always possible to distinguish between *Ulmus americana* and *U. rubra*, or between *Fraxinus americana* and *F. pennsylvanica*, so they were combined into two-species groups.

Stems < 1.5 m tall were inventoried in two 1-m wide transects that were established on the outsides of the $Y=5$ and $Y=15$ -m lines, parallel to the long axis of the plot (Fig. 1). A single tape measure was pulled taut along each line and, beginning from one end, each woody stem ≥ 20 cm tall and < 1.5 m tall within one meter of this line was tallied to species or genus (where species could not be accurately determined). A meterstick was used to determine the outer boundary of the transect and to place each individual stem into one of 2 size classes: 20–50 or 50–150 cm tall. All individual stems arising from ground level were tallied, even when multiple stems arose from a common rootstock. Due to uncertainties of species-level identifications, we did not distinguish among *Ribes* spp., *Rubus* spp., or *Vitis* spp. We combined all native *Rosa* spp. and all native *Lonicera* spp. into single-genus groups (*L. tartarica* including *L. maackii* Maxim. and *R. multiflora* were distinguished). Because *Rubus* and *Ribes* have arching branches that occasionally root at their tips, we recorded all stems longer than 50 cm as being in the 50–150 size class, even when they were > 1.5 m long.

Finally, we searched the entire plot for any additional species that were present in the < 1.5 -m-tall categories but which were not tallied in the 1-m wide transects. These species were presumed to have an abundance of one per plot in each size class in which they occurred. The total number of other individuals < 1.5 m tall within each plot was determined by multiplying the transect tallies by 10. Altogether we recorded the species and abundance of all woody plants ≥ 20 cm tall in 67 plots, and recorded the species, size and location of all trees and vines > 2.5 cm dbh (i.e., ≥ 8 cm cbh) in 86 plots.

Our aim has been the development of a methodology that is both time- and cost-efficient, that is accurate, and that provides both species tallies and abundance data. Every plot is different, but on average a field team of two persons using these techniques can establish permanent markers, record physical characteristics, and inventory all woody vegetation ≥ 20 cm tall in two 0.1-ha plots in a single 8-hr field day, excluding travel time to and from sites.

Data analysis

To evaluate species-site relationships and to identify the major forest types observed, we applied classification and ordination techniques (Gauch 1982). For these purposes we included only species > 2.5 cm dbh. We used relative basal area as a measurement of species abundance, transformed using an octave scaling (e.g., Hill 1979a). Basal area is a good measure of a species' dominance of resources within a site and correlates well with subjective visual im-

pressions of forest composition. Classification of forest community types was conducted using the default parameter values of TWINSPAN (Hill et al. 1975, Hill 1979b). TWINSPAN uses the species abundance data from each plot to split all plots within a group (beginning with all plots) into two most-dissimilar groups, and sequentially repeats this process with each defined group.

We applied detrended correspondence analysis (DECORANA, Hill 1979a, Hill and Gauch 1982, Peet et al. 1988) to evaluate better the compositional relationships among the forest plots and among tree species. We applied the same transformations as described for the TWINSPAN analysis and used the default parameter settings for the analysis. DECORANA uses the plot-species data matrix to generate multivariate axes that sequentially explain the greatest amount of variability among plots. The program produces axis scores (i.e., values) for each plot and for each species. The generated plot scores represent the weighted scores of species present in each plot, and the species scores represent the species position along the defined multivariate axes.

To characterize the species composition of different forest types, we calculated species importance values for each major group delineated by TWINSPAN. We calculated relative frequency, abundance, and dominance for each species and totaled these values to determine the species' overall importance value (I.V.). For each species x in each forest group:

frequency(x)

$$= \frac{\text{number of plots containing } x}{\text{total number of plots}}$$

relative frequency(x)

$$= \frac{\text{frequency of species } x}{\text{total frequency of all species}} \times 100$$

relative abundance(x)

$$= \frac{\text{number of individuals of species } x}{\text{total number of all individuals}} \times 100$$

relative dominance(x)

$$= \frac{\text{total basal area of species } x}{\text{total basal area of all species}} \times 100$$

I.V.(x)

$$= \text{rel. frequency}(x) + \text{rel. abundance}(x) + \text{rel. dominance}(x).$$

The sum of importance values so calculated is 300 for each forest type.

RESULTS

We encountered 66 species and genera of woody plants in the 86 tenth-hectare permanent plots that we established in central Iowa. Forty-five species were encountered at sizes >2.5 cm in diameter, and 30 species were encountered that had diameters (dbh) of ≥ 10 cm (Fig. 2). More than 85% of the stems tallied were <150 cm tall, and 98% were <10 cm dbh. Many of these smaller stems were non-tree species, and 20% of all tallied stems were *Ribes* spp. The distribution of all stems shows a typical log-linear decline in stem abundance with increasing size (Fig. 3), with a couple of notable breaks. Between the <150 cm-tall and the ≥ 150 cm-tall size classes the number of stems declined by 80%, whereas the number of species declined by only 2. Also, in going from the 2.5–10 cm-dbh size class to the 10–20 cm-dbh size class, stem numbers declined by

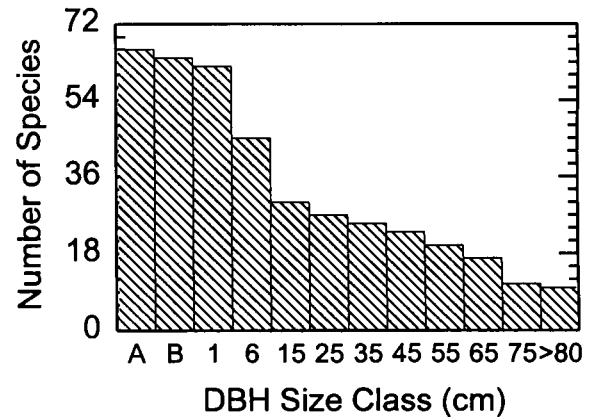


Fig. 2. The number of species inventoried in relation to the minimum size included in the survey. A total of 66 species reaching a size of 20 cm tall were encountered in the current study. Only 30 species exceeded a dbh of 10 cm. As the minimum size class included in the survey is increased, fewer species are included. "A" refers to stems ≥ 20 cm tall, "B" refers to stems ≥ 50 cm tall, "1" refers to stems ≥ 1.5 m tall, and all other numbers refer to the midpoints of diameter classes.

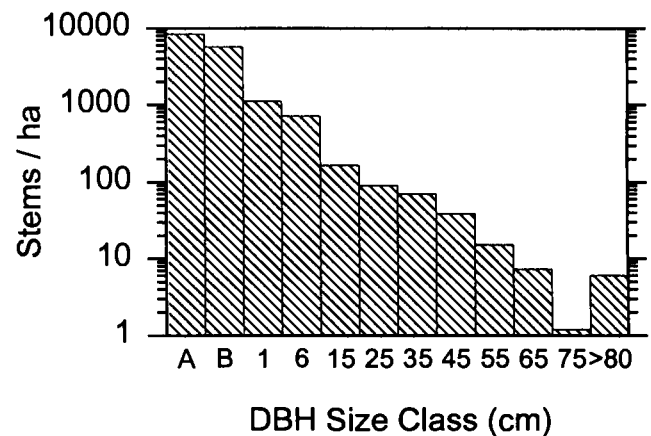


Fig. 3. Size-class histogram of all woody stems inventoried in the 67 forest plots in central Iowa in which stems ≤ 2.5 cm dbh were measured. "A" refers to stems ≥ 20 cm tall but <50 cm tall, "B" refers to stems ≥ 50 cm tall but <1.5 m tall, "1" refers to stems ≥ 1.5 m tall but ≤ 2.5 cm dbh, and all other numbers refer to the midpoints of diameter classes.

$>75\%$, while the number of species declined by only 33% (cf. Fig. 2 & 3).

Taken together, the 86 forest plots contained an average of 370 stems/ha that were ≥ 10 cm dbh, and had an average total basal area of 28.3 m²/ha. The most abundant species were *Ostrya virginiana*, *Quercus alba*, *Q. rubra* L. (= *Q. borealis* Michx. f. var. maxima (Marsh.) Ashe), *Tilia americana*, *Acer nigrum*, and *Carya ovata*. Each of these species had an average of >25 stems/ha that were ≥ 10 cm dbh. Several species were encountered very frequently: *Ostrya virginiana* occurred in 68 of the 86 plots, *Tilia americana* in 63, *Quercus rubra* in 60, *Carya ovata* in 59, *Ulmus americana* in 58, and *Quercus alba* in 55. Species richness of stems >2.5 cm dbh ranged from 4–17 per plot, and averaged ten per plot. There was an average of 6 trees/ha that were ≥ 80 cm dbh. There were relatively few dead trees, par-

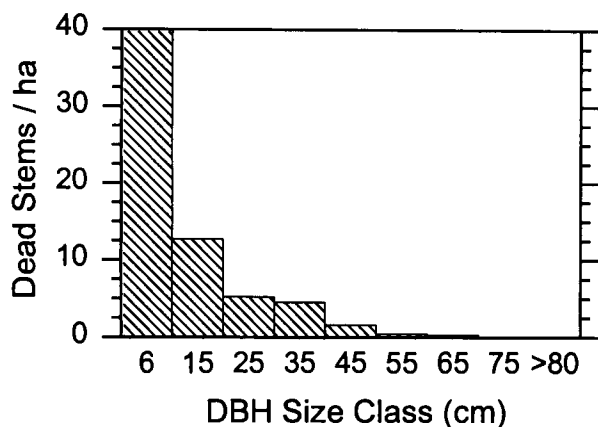


Fig. 4. Size-class distribution of standing dead tree stems >2.5 cm dbh. These data are derived from complete inventories of trees in 86 tenth-hectare plots in central Iowa.

ticularly in the larger size classes: there was on average <1 dead tree/ha that was ≥ 50 cm dbh (Fig. 4).

Classification of the plot data with TWINSpan generated an initial split that effectively distinguished upland stands from bottomlands. Twenty plots were distinguished based on the presence of *Juglans nigra* and an abundance of *Celtis occidentalis* and *Ulmus americana*. This group included the fourteen plots that we classified as bottomland stands in the field, as well as six upland stands containing species typically found in bottomlands. We hereafter refer to this group as bottomland hardwoods.

The remaining 66 plots were characterized by an abundance of *Ostrya virginiana*, *Quercus alba*, and *Q. rubra*, and by the presence of *Carya ovata*, and will be referred to as the upland group. Further splitting of the upland forest group by TWINSpan generated a division between plots that contained an abundance of *Acer nigrum* and *Quercus rubra* (with *Fraxinus nigra* and *Amelanchier arborea*) (41 plots), and plots containing *Prunus serotina* and abundant *Ulmus americana* (25 plots). We will refer to these two groups as mesic and dry upland forests, respectively, because previous work has shown that this difference correlates with annual solar insolation as estimated from slope and aspect measurements (Sin 1996), and insolation is a good measure of relative site aridity in upland stands. *Carya ovata*, *Quercus alba*, *Ostrya virginiana*, *Fraxinus americana*, and *Tilia americana* were frequent in both upland forest groups. Because these species had a relatively low fidelity for specific sites, they had little influence on this TWINSpan division of upland forest types.

The three forest groups identified by TWINSpan shared many species. Of the 23 species most important species, 14 were present in all three forest groups (Table 1). The bottomland hardwoods differed substantially from the upland forests in having a greater importance of *Acer negundo*, *A. saccharinum*, *Aesculus glabra*, *Celtis occidentalis*, *Gymnocladus dioicus*, *Juglans nigra*, but relatively low importance values of *Carya ovata*, *Ostrya virginiana*, *Quercus alba*, and *Q. rubra* (Table 1). Floristic differences between the two upland groups consisted primarily of differences in relative importance among species (Table 1). Mesic uplands had a greater importance of *Acer nigrum*, *Amelanchier arborea*, *Carpinus caoliniana*, *Fraxinus nigra*, *Quercus rubra*, and *Tilia americana*, whereas the dry uplands had higher importance values of *Prunus serotina*, *Quercus alba*, and *Ulmus* spp.

The bottomland hardwoods, dry uplands, and mesic uplands groups defined by TWINSpan are displayed on the ordination diagram produced from DECORANA (Fig. 5A). Eigenvalues for axes 1 and 2 were 0.422 and 0.221, respectively. Additional axes ex-

Table 1. Species importance values in the three general forest groups defined by TWINSpan. Only species with an importance value ≥ 5 in at least one forest group are included, based on tallies of all stems >2.5 cm dbh.

SPECIES	DRY UPLANDS (N = 25)	MESIC UPLANDS (N = 41)	BOTTOM-LAND HARDWOODS (N = 20)
<i>Acer negundo</i>	0	1	11
<i>A. nigrum</i>	4	35	24
<i>A. saccharinum</i>	0	0	7
<i>Aesculus glabra</i>	2	0	8
<i>Amelanchier arborea</i>	1	8	0
<i>Carpinus caroliniana</i>	1	9	0
<i>Carya cordiformis</i>	9	9	12
<i>C. ovata</i>	24	16	3
<i>Celtis occidentalis</i>	12	6	37
<i>Crataegus</i> spp.	0	0	5
<i>Fraxinus americana</i>	13	11	15
<i>F. nigra</i>	0	9	2
<i>F. pennsylvanica</i>	0	2	5
<i>Gymnocladus dioicus</i>	0	0	6
<i>Juglans nigra</i>	3	3	36
<i>Ostrya virginiana</i>	56	60	8
<i>Prunus serotina</i>	8	1	6
<i>Quercus alba</i>	73	26	2
<i>Q. macrocarpa</i>	6	2	8
<i>Q. rubra</i>	21	46	6
<i>Tilia americana</i>	14	31	16
<i>Ulmus americana</i>	16	7	32
<i>U. rubra</i>	15	7	17

plained little of the variability among plots and will not be discussed. This figure (5A) suggests three trends. First, only 20 of the 86 plots were identified as bottomland hardwoods by TWINSpan, yet these plots occupy the entire right half of Fig. 5A. This means that half of the total floristic variability that we encountered among all plots was due to variability within the bottomland hardwoods group. Second, there was relatively less variability among upland (mesic and dry) forest plots along axis 1. The upland plots varied more along axis 2, with the mesic plots having higher axis 2 scores than dry plots (Fig. 5A). Third, there was little separation between the two upland groups. The upland plots varied in a continuum along axis 2.

Comparisons of plot and species scores obtained from ordination (Figs. 5A, 5B and 5C) allow for better visualization of site-species relationships. Species with high axis-1 scores were more abundant in plots with high axis-1 scores, and vice versa. High axis-1 scores are typical of species that colonize disturbed locations, including *Acer negundo*, *Crataegus* spp., *Fraxinus pennsylvanica*, *Gleditsia triacanthos*, *Gymnocladus dioicus*, *Juglans nigra*, and *Morus* spp. (Fig. 5B and 5C). In contrast, most of the common upland canopy-tree species (and plots) had lower axis-1 scores (Fig. 5A and 5B).

There was a large amount of species overlap among upland forest plots. Considering only trees >2.5 cm dbh, *Quercus alba* occurred in 52 of the 66 upland forest plots, *Q. rubra* in 54, and both species occurred together in 42 upland plots. *Carya ovata* occurred in 55 of the 66 upland plots, *C. cordiformis* in 33, and they occurred together in 28 plots. As a result, many of the species had axis 1 and 2 scores lying together in the middle of Fig. 5B. *Ulmus americana* and *U.*

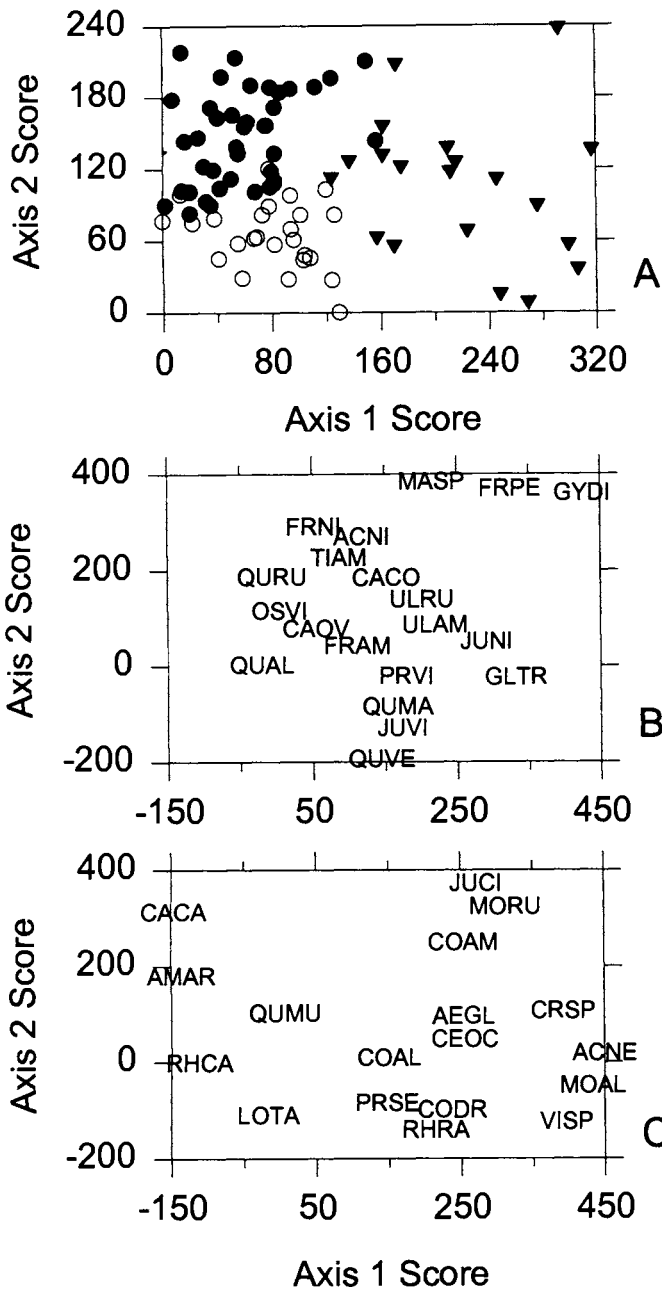


Fig. 5. Ordination diagrams of plot and species scores along DECOR-ANA axes one and two, based on the inventory of woody species >2.5 cm dbh in 86 forest plots. In (A) all plots are shown with respect to their TWINSPAN classification as mesic uplands (solid circles), dry uplands (open circles), or bottomland hardwoods (solid triangles) stands. (B) and (C) show individual species, labeled by the first two letters of the genus and species: ACNE=*Acer negundo*, ACNI=*A. nigrum*, AEGL=*Aesculus glabra*, AMAR=*Amelanchier arborea*, CACA=*Carpinus caroliniana*, CACO=*Carya cordiformis*, CAOV=*C. ovata*, CEOC=*Celtis occidentalis*, COAL=*Cornus alternifolia*, COAM=*Cor-ylus americana*, CODR=*Cornus drummondii*, CRSP=*Crataegus* spp., FRAM=*Fraxinus americana*, FRNI=*F. nigra*, FRPE=*F. pennsylvanica*, GLTR=*Gleditsia triacanthos*, GYDI=*Gymnocladus dioicus*, JUCI=*Juglans cinerea*, JUNI=*J. nigra*, JUVI=*Juniperus virginiana*, LOTA=*Lonicera tatarica*, MASP=*Malus* sp., MOAL=*Morus alba*, MORU=*M. rubra*, OSVI=*Ostrya virginiana*, PRSE=*Prunus serotina*, PRVI=*P. virginiana*, QUAL=*Quercus alba*,

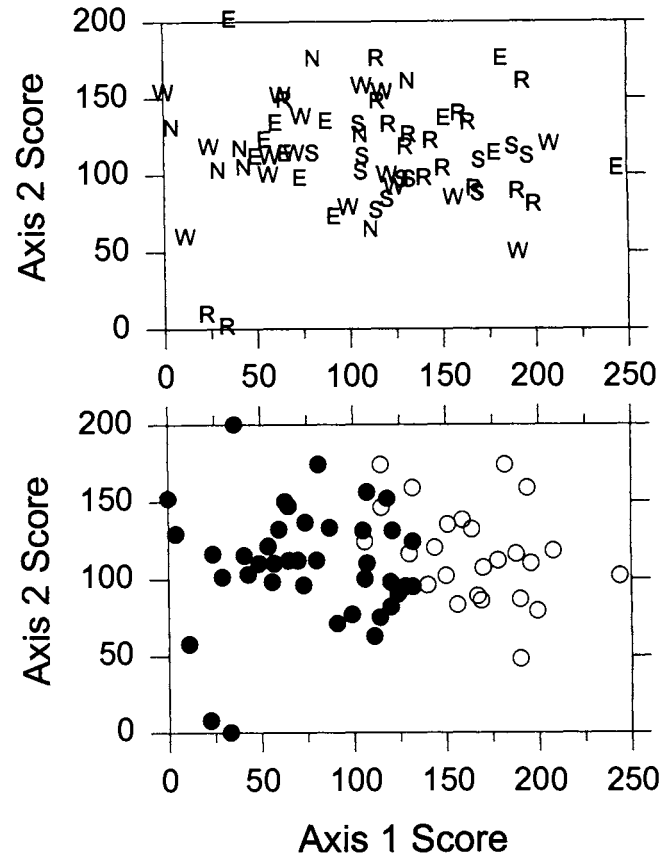


Fig. 6. Ordination diagram of 66 upland forest plots of central Iowa, shown according to their topographic positions. Key to top graph: R=Ridgetop, N=north- and northeast-facing aspects (340-70°), E=east- and southeast-facing slopes (70-160°), S=south- and southwest-facing slopes (160-250°), W=west- and northwest-facing slopes (250-340°). Key to lower graph: solid circles = mesic upland plots, open circles = xeric upland plots, as delineated by TWINSPAN.

rubra were found together in 43 of the 86 plots and were both absent from 14 plots, suggesting that these congeners favored the same habitats.

Nevertheless, some consistent trends were evident. Both *Fraxinus pennsylvanica* and *F. nigra* had higher axis 2 scores than did *F. americana*, *Carya cordiformis* had a higher axis 2 score than did *C. ovata*, and *Q. rubra* had a higher axis 2 score than did *Q. alba*. Likewise, both *Acer nigrum* and *Tilia americana* had relatively high axis-2 scores. Hence, mesic sites (as indentified by TWINSPAN) tended to contain relatively more *Acer nigrum*, *Carya cordiformis*, *Quercus rubra*, and *Tilia americana*; whereas the dry forest types contained relatively more *Carya ovata*, *Fraxinus americana*, and *Quercus alba* (see also Table 1).

We conducted an additional ordination that included only the 66 upland forest plots, to better identify relationships between the mesic and xeric groups. The results of this ordination (Fig. 6) show again

←
QUMA=*Q. macrocarpa*, QUMU=*Q. muehlenbergii*, QURU=*Q. rubra*, QUVE=*Q. velutina*, RHCA=*Rhamnus cathartica*, RHRA=*Rhus radicans*, TIAM=*Tilia americana*, ULAM=*Ulmus americana*, ULRU=*U. rubra*, VISP=*Vitis* spp. Some locations are offset slightly to increase legibility.

the continuum of variability in upland forests. East-facing and west-facing slopes occur throughout the ordination diagram. However, north-facing slopes had significantly lower axis-1 scores than did south- and southwest-facing slopes (t -test, $P < 0.005$). Ridgetops clustered with southerly aspects, with the exception of two plots from Hardin City Woodland that had very low axis 1 and 2 scores (Fig. 6). This suggests that there were consistent floristic differences between the most mesic (i.e., northerly) and the most xeric (i.e., southerly) aspects. However, stands on intermediate aspects (east and west) did not have intermediate scores, and varied with no discernible trends (Fig. 6).

DISCUSSION

The broad characterization of central Iowa forests presented here indicates how data from permanent plots provide insights into the overall composition and structure of our forests. Additional analyses can relate composition and structure to measured soil and site properties, can answer questions of species dynamics (e.g., maple vs. oak regeneration), and can allow for comparison of forests from different areas. Further, permanent plots provide a valuable aid to future resource managers and scientists interested in vegetation changes and their causes. The plot placement and inventory methods described here present a minimum effort needed to address such questions and are recommended for use throughout the state.

Our current analyses of 86 plots suggests that central Iowa forests consist of two major types: bottomland hardwoods and upland forests, with the latter displaying a continuum of variation.

Bottomland hardwoods

The 20 plots in the bottomland hardwoods group were typified by *Juglans nigra*, *Celtis occidentalis* and *Ulmus americana*. However, several additional species had a high fidelity to this group, including *Acer negundo*, *Acer saccharinum*, *Crataegus* spp., *Gleditsia triacanthos*, *Gymnocladus dioica*, and *Populus deltoides*. This group included six plots that were classified as uplands based on their topographic positions, but which contained species indicative of bottomlands. These upland plots varied, but included an old hillside slump, low terraces near streams, and sites that were probably formerly grazed woodlands with relatively open canopies. The major environmental factor(s) causing these plots to differ from the other upland plots is probably disturbance history. Higher axis-1 scores in our ordinations (Fig. 5) likely correlate with an increasing frequency and magnitude of canopy-opening disturbances. Indeed, many of the species having high axis-1 scores (e.g., *Acer negundo*, *Celtis occidentalis*, *Crataegus* spp., *Gleditsia triacanthos*, *Morus* spp.) are frequently encountered in young secondary woodlands, both upland and bottomland, throughout central Iowa.

One feature that clearly separates true bottomland sites from the upland forests of Iowa is the nearly complete absence of species such as *Quercus alba*, *Q. rubra*, and *Ostrya virginiana*, which are widespread in upland sites. Possibly, these species cannot tolerate flooding or bottomland soil conditions. However, even small topographic rises sometimes support upland species within otherwise pure bottomland stands.

The relatively high diversity among bottomland hardwood sites (e.g., Fig. 5A) is due most likely to habitat diversity associated with the size of floodplains and the frequency, timing, and duration of flooding events, as well as proximity to seed sources and chance colonization events. Erosional processes that continually create canopy openings and new habitat for colonization and growth near stream edges are also important (e.g. Kupfer and Malanson 1993).

Upland forests

The floristic patterns we observed within the upland forests are consistent with previous descriptions of central Iowa's forests (e.g., Aikman and Smelser 1938, Braun 1964, Sanders 1968, Niemann and Landers 1974, Bach 1982, Johnson-Groh 1985). In general, our data suggest broad similarities in the composition of upland forests, with *Ostrya virginiana* being particularly ubiquitous. The widespread occurrence of many species and the overlapping distributions of congeneric species, despite plot selection that minimized within-plot environmental heterogeneity, suggest that most of our upland forest tree species grow in a wide variety of habitats.

We found and inventoried both black maple-basswood forest stands and white oak-shagbark hickory forest stands. However, these types represented points along a continuum rather than discrete forest community types. The majority of our plots could not be designated as one or the other of these types (Fig. 5A). The upland plots included a broad continuum of species compositions, as previously suggested by Sanders (1968). We are not suggesting that there is no predictability as to where species occur within the upland forests of central Iowa, but rather that predictability is limited. Plots on northerly aspects did differ from those on southerly aspects (Fig. 6), suggesting consistent differences between the most mesic and driest sites. However, plots on other aspects were not intermediate in composition. This suggests that factors other than those associated with aspect, e.g., valley width, disturbance history, seed sources, etc., were more important in determining species composition on these aspects. Further analysis of species-site relationships within central Iowa forests is needed.

An important factor that we were not able to document was disturbance history. We frequently observed distinct changes in forest composition across old fence lines that were not associated with habitat differences. Historical impacts have no doubt affected the sites we inventoried. In many cases past disturbances may be more responsible for the current vegetation than are current habitat conditions.

We did not randomly select our forest sites or plot locations within forests, and some of our results reflect this. For instance, we found an average of 6 trees/ha that were ≥ 80 cm dbh. This may be an inflated estimate of the average density of large trees, due to site selection that favored old groves and mature stands. We also found < 1 standing dead tree/ha that was ≥ 50 cm dbh, although our sampling was not obviously biased against dead trees. A lack of standing dead trees, an overall scarcity of large dead timber on the ground, and an abundance of large living trees are all suggestive of forests that have not yet matured.

Despite our attempts to locate and inventory the oldest and least-disturbed forest stands, even the oldest forests of central Iowa are secondary forests lacking the attributes of true old-growth stands. It may be most appropriate to consider all of central Iowa's forests as still relatively young and still in the process of recovering from disturbances that occurred earlier in this century. We can expect that both the structure and composition of these forests will change: the permanent plots we established will allow for documentation and analysis of this change.

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