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Using Releves for Silvicultural Interpretation

Background

Releves are plots that we use to sample vegetation in ecologically intact and generally mature forests in Minnesota. Since the 1960s, releves have been collected for the purpose of classifying and understanding native vegetation. Initial efforts were aimed at conservation and education, but as the corpus of data grew we recognized the opportunity to use releve data as guidance for active, if not intensive management of forests. This chance was evident when management guides, developed from what are essentially releves, appeared across the Great Lakes Area in the form of American habitat-types (Coffman, et al. 1984; Kotar and Burger, 1988, 1996, 2000) and Canadian forest ecosystems (Sims et al.1989. Harris et al. 1996.). Releves are the basis our Native Plant Community (NPC) classification (MN DNR 2003, 2005, 2005), which we use to communicate management needs and strategies.

Because releves are the basis of our classification there is no need to model their assignment to an NPC Class as we did for the PLS and FIA interpretations. Most of the data used for silvicultural inference are summary calculations based upon the whole set of releves that belong to an NPC Class. Beyond classification, we felt that we could wring silvicultural information from releves in three general areas:

1. How "suitable" trees are for each NPC Class (i.e. matching species to site)
2. How successful trees are in developing advance regeneration and recruiting to higher strata (i.e., an assessment of how site affects natural regeneration opportunities)
3. How advance regeneration of trees co-associates with parent trees and other plants (i.e. recognizing plants and situations that are either competitive with or beneficial to tree establishment)

Data

Releve data, collection methods, and applications are covered in detail in *A Handbook for Collecting Vegetation Data in Minnesota: the Releve Method* (MN DNR, 2007). Below, we present just enough of the method so that one can understand how we constructed our silvicultural tables.

Distribution

Releves are not distributed randomly or systematically across the landscape. This means that they can't be used to predict how much of a community occurs in the state or a county. That is, they are not a forest inventory. Rather, the goal was to sample as evenly as possible the full range of environmental conditions that naturally cause one forest to be different from another. Presumably, the vegetational differences are reflective of function – how water and nutrients cycle in a forest class, how trees naturally regenerate, how succession proceeds, how soil properties affect operability, etc. These things, in conjunction with the traditional life-history and physiology of tree species, are the essence of silvicultural understanding.
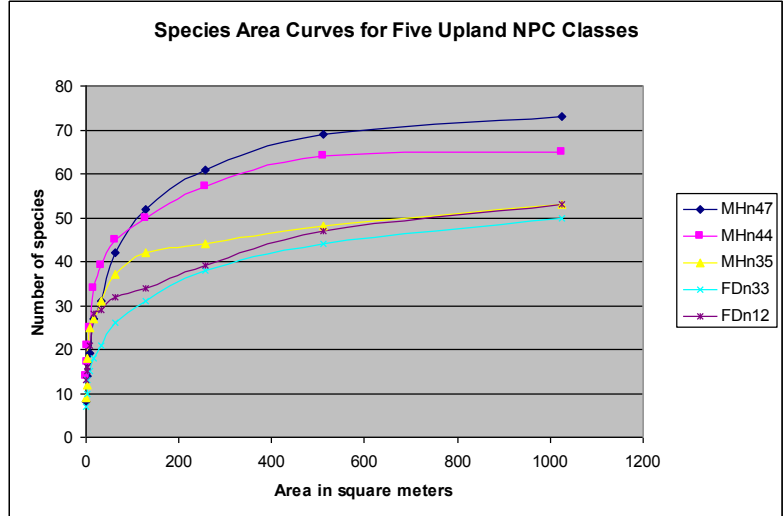
Releves are subjectively located in forests away from obvious human disturbance and in areas that seem homogeneous and typical of the stand. Statewide, we attempted to balance the sampling along ecological gradients that affect vegetation – soil drainage, parent material, slope, aspect, landform etc.
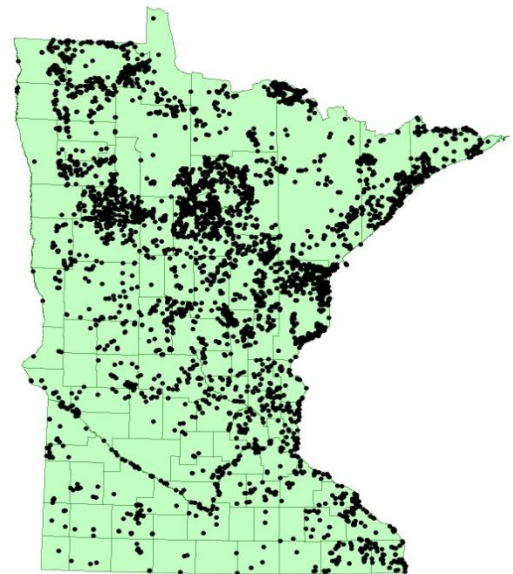
Location of about 9,000 releves in Minnesota as of August 2009.

Size

Most of our forested releves were collected on large, 400m^2 plots except for some 100m^2 plots on the Chippewa National Forest and some early releves of indefinite size. By comparison to other sampling methods, these are large plots. This is so, because species/area plots in typical Minnesota forests show that plots must be this large to capture about 70-90% of the plants in a homogeneous area of the typical 20-acre stand. This is important because most foresters tend to traverse an entire stand before making management decisions and releves are reasonably representative of the stand. Apparently, plots of this size are large enough to include most of the fine-scale pattern of the groundlayer as it relates to tree crowns, clone size, cradle-and-knoll topography, hummock and hollows in peatlands, nurse logs, seedling "safe sites," etc.

Species Area Curves for Five Upland NPC Classes

Legend: MHn47, MHn44, MHn35, FDn33, FDn12

X-axis: Area in square meters
Y-axis: Number of species

Species area curves for five upland forest NPCs (above). Note that the curves are relatively flat at 400m^2 and that expanding plots from that point tends to yield few additional species.

Releves are large plots designed for classification of vegetation and communication of concepts at a scale meaningful to foresters when examining stands. They may be used for analysis of tree suitability, advance regeneration, and species association, but it is important to keep their size in mind when interpreting the results. Releves are slightly too small for analysis of tree recruitment and they are slightly too large for analysis of association where plant interaction is assumed.

Strata

The initial step in describing the vegetation on the plot is to identify the vertical strata on the plot. The convention in Minnesota is to follow the physiognomic system of Kuchler (1967). The strata are combinations of life-form and the height class(es) that they occupy. Examples of life-forms that one would find in a forest are: E=needle-leaf evergreen woody plants like pines, D=broadleaf-deciduous woody plants like oaks and hazelnuts, G=graminoids including grasses, sedges, and rushes, H=forbs including ferns, fern allies, and most wildflowers. The height strata are in 8 classes that widen with height: 1=<0.1m, 2=0.1-0.5m, 3=0.5-2m, 4=2-5m, 5=5-10m, 6=10-20m, 7=20-35m, 8=>35m. The goal is to describe the actual strata that have formed and not be compelled to describe each of these arbitrary classes. Thus, contiguous height classes are to be combined if there is no break at the standard seam(s) between them, and height classes are skipped if there is little leaf area in them. On the right is an example of physiognomic strata that might be seen in a mixed hardwood-conifer forest.

Sampling by stratum allows us to use releves for analysis of tree recruitment.

Figure 8. Delineation of height classes in forested relevé plot.

MN DNR, 2007
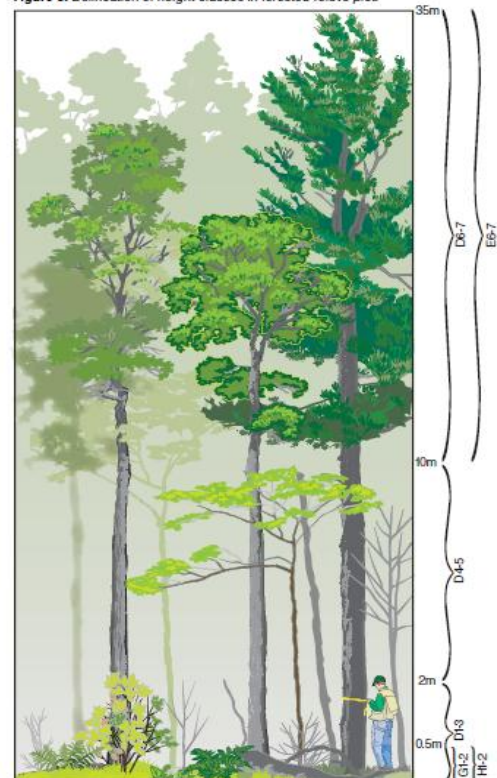
Plant Records

Within each stratum, all of the component vascular plants and ground-covering mosses are recorded. Field ecologists estimate the cover of each species in a stratum by visually placing them in one of 7 cover/abundance classes: r=<5% cover, single individual; +=<5% cover, several individuals; 1=<5% cover, numerous individuals; 2=5-25% cover; 3=25-50% cover; 4=50-75% cover; 5=>75% cover. For analysis, cover class ranges were converted to a single number by using mid-points of cover classes and by assigning cover values to the initial 3 abundance classes as follows: r=1%, +=3%, 1=5%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%.

Figure 7. Example of physiognomic group.

ID	C.S	SPECIES NAME	REMARKS
		E 4 – 6 c	
2	4.1	Pinus strobus	FR
2	r.1	Abies balsamea	DF, BR
4	+.1	Picea cf. glauca	#1

Typical block of species records for needleleaf evergreen trees, 2-20m tall, with combined cover of 50-75% (E4-6i stratum). Variables: ID=code for reliability of identification, C=cover class, S=sociability code, SPECIES NAME=scientific epithet, REMARKS=remark codes. MN DNR 2007.

Individual plant records in releves allow us to calculate a species' presence, mean cover-when-present, co-occurrence with other species, and plot synecological scores for our interpretations.

Creating the Databases for Native Plant Community (NPC) Silvicultural Interpretations

Suitability Database and Analysis

We wanted to create a tool to help foresters determine which species of trees are "suited" to site conditions in an area they wish to manage. In mixed stands, selecting the species to favor over others is one of the most common decisions made by a forester – thus our tool must allow for comparison and ranking of species. Because some valuable species have been lost from sites after a few rotations, foresters often wonder if some species would succeed if they were introduced to the site – thus our tool must also accommodate cases where trees are absent but the community of groundlayer plants and soils would suggest that it is appropriate habitat.

We chose to create a suitability index (SI) for all plants, not just trees. We did this because we suspect that understory plants with a high index are likely to compete with tree seedlings. This helps us focus on species with the potential to achieve seedling-smothering abundance and write prescriptions to mitigate their effect. Conversely, recognizing that the understory is composed of plants with a low index helps to avert costly control efforts. We chose also to treat tree regeneration (<10m tall) as a species separate from canopy trees (>10m tall). Disparity between a species' regeneration SI and its tree SI is an indication of the effectiveness of seed trees in mature stands.

Suitability was calculated for all plants in a Native Plant Community Class, not just trees. Tree regeneration was treated as a species separate from canopy trees.

One element of suitability is commonness. A plant is suited to a community if we often find it there. The most common measurement is presence, which is just the percentage of the sample plots that contain the species.

Presence= (number of releves with the plant present / total number of releves for the community) * 100

Active management tends to obscure natural presence because some species are favored over others by intent or indirectly by replacing natural disturbances with timber harvesting. For suitability to have predictive value of plants that would do well in a community if given a chance, we need another element. We chose to use mean cover-when-present (MCWP) as a measure of suitability of infrequent species because it helps weight species that do well when given the chance.

MCWP=sum of all cover percents for the plant / number of releves with the plant present

In order to create a single index for suitability (SI), presence and MCWP must be either added or multiplied. We chose to multiply because it yielded higher scores for trees that we know can grow at commercial abundance in the communities.

$$Raw\ SI = Presence * MCWP$$

The raw suitability index (SI) for a plant is the product of its presence and mean cover-when-present in Native Plant Community Class. Plants have high index values when we often find them in that community and also because they are usually abundant.

By chance, especially for communities with fewer releves, the ranges of raw SI scores differ among NPC Classes. In order to compare a plant's SI among all the communities, we had to re-scale the raw SI scores so that they have the same range. This was done by first eliminating all species with <5% presence to get rid of the long tail of very infrequent species with near zero SI scores in the distribution. The plants with >5% presence were then ranked and re-scaled so that rank positions ran from zero to five. The ranking was divided into five equal classes as follows:

Suitability Index	Equivalent Percentile	Descriptor
0-1	0-20%	none
1-2	20-40%	Poor Suitability
2-3	40-60%	Fair Suitability
3-4	60-80%	Good Suitability
4-5	80-100%	Excellent Suitability

To compare the suitability indexes of just trees, all non-trees were removed from the dataset, sorted by descending SI, and then assigned their consecutive rank order. The species with the highest SI was given the rank of 1, the species with the second highest SI was given the rank of 2, etc. A table with rows of all common trees (>5% presence in at least one community), and columns for all wooded NPC Classes was constructed and published as a field tatum guide to suitability (MN DNR, 2006).

The raw suitability indices were re-scaled so that rank order runs from zero to five. This is done so that a tree's index in one Native Plant Community Class can be compared to another Class. Trees were then ranked by their suitability index to facilitate selection of better crop trees.

When applying SI estimates for crop tree selection, it is important to keep the origin of the data in mind. Releves come from natural mature forests. Natural means that the plant cover is largely native, and that releve plots are placed away from field edges, clearcuts, roadsides, and other anthropogenically disturbed areas (MN DNR 2007). There is bias towards sampling virgin timber in the dataset, but virgin forest is so rare that the overwhelming majority of forest releves occur in second-growth stands showing some continued removal. The consequence of using releves to estimate suitability is that the index reflects tree performance with little or no silvicultural intervention. If the management goal is to work with the community's natural momentum with minimal disturbance, then the SI estimates are especially predictive. Trees with low SI are not necessarily unsuited for a site if there is a commitment of continued silvicultural intervention in the form of site preparation, protection, weeding, release, etc. A low SI estimate also does not mean that a tree would do poorly if the stand were in another growth stage. Our index values are mostly from forests 40-100 years old and success in the form of high presence and abundance at that age could be the consequence of either success at initiation or success in replacing an initial cohort. For any community exhibiting relay-floristic succession, SI values would differ among young, mature, and old growth sample sets.

Suitability index is most meaningful when little silvicultural intervention is anticipated beyond removal – simple removal being the most common origin of stands sampled by releves.

Natural Regeneration Database and Analysis

The vertical structure of releves was used to interpret the ability of trees to establish themselves and recruit to higher strata under the canopy of a mature forest and on seedbeds associated with older forests. The goal was to develop an appreciation of which trees are capable of developing enough advance regeneration to fully stock a future stand by natural regeneration. For trees with modest advance regeneration, we wanted to figure out if the problem seems to be related to poor establishment or poor recruitment – issues that can be resolved by underplanting or intermediate treatment. For trees with little or no advance regeneration we assume that even-aged systems would be required to perpetuate them in that community.

The tree height data from releves was transformed into 4 standard height strata: regenerants <10cm tall, seedlings 10cm – 2 m tall, saplings 2–10m tall, and trees >10m. These height breaks were used because they are the most frequently used on releves to describe the natural structural breaks in forests. Still, some releves report strata that span our standard height seams and we had to apportion the presence of the tree and its percent cover into our standard classes. This was done by splitting the reported strata into the 8 individual height classes and evenly splitting the cover among the classes. For example, sugar maple reported in a D3-6 layer (0.5-20m) comprises four individual height classes that need to contribute cover to our standard seedling, sapling, and tree strata. The cover of sugar maple in that stratum was class 3 (25-50% cover). Using the mid-point rule as for suitability (see above), cover class 3 is converted to 37.5%, and the apportionment is 37.5% / 4 = 9.37% cover awarded for sugar maple in each height class. After cover was awarded to all individual height classes in a releve, they were then lumped into the standard strata and the individual covers summed.

The initial step of the analysis was to create a dataset of just trees and their cover in 4 standard height strata: regenerants <10cm tall, seedlings 10cm to 2m tall, saplings 2 to 10m tall, and trees >10m.

For each standard stratum we calculated an index of "regeneration success" for the tree species. We settled on three measures of success:

First, trees were considered successful if they were *common* in a particular stratum. Presence is our measure of stratum commonness, and below is how seedling presence was calculated.

SE Presence= (# of releves with the tree present as a seedling / total # of releves for the community) * 100

Second, trees were considered successful if we found them to be *abundant* in a particular stratum. Mean cover-when-present (MCWP) was our measure of stratum abundance, and below is how seedling MCWP was calculated.

SE MCWP=sum of all seedling cover of tree / number of releves with the tree present as a seedling

Third, trees were considered successful recruiters if we often found it in *multiple strata*. As a measure of recruitment complexity we calculated the mean number of strata when present (MSWP) reported in the original releves (not our standard strata) for a species. We used this number as a weighting factor to help segregate species that develop a presence in many layers from those that don't develop a lot of strata because they probably need some kind of disturbance to develop an understory cohort.

MSWP = sum of all reported strata for a species / number of releves in which the species occurs

From these three measures of stratum success we calculated the raw recruitment index by multiplying the numbers together. Below is how the raw seedling index was calculated.

Raw SE Index = SE presence * SE MCWP * SE MSWP

Commoness (presence), abundance (mean cover-when-present), and complexity (mean strata-when-present) were used to estimate the success of tree species as regenerants, seedlings, saplings, and parent trees.

For each stratum – regenerants, seedlings, saplings, and trees – the ranges of raw index scores are different and not comparable between strata and between communities. To allow comparison, the raw scores were ranked and then re-scaled so that the lowest raw score was zero and the maximum was five.

> *The raw regeneration indices were re-scaled so that rank order runs from zero to five. This is done so that a tree's index in one stratum can be compared with other strata for the same NPC Class and so that the indices can be compared across NPC Classes.*

The indices of regeneration were placed into classes as for suitability so that in tables, foresters can quickly identify the species that tend to have poor, fair, good, or excellent regeneration in mature forests that have not been silviculturally manipulated in the recent past.

Regeneration Index	Equivalent Percentile	Descriptor
0-1	0-20%	none
1-2	20-40%	Poor Suitability
2-3	40-60%	Fair Suitability
3-4	60-80%	Good Suitability
4-5	80-100%	Excellent Suitability

Species Associations Database and Analysis

Because all plants seem to use the same resources – water, nutrients, light – it is understandable that foresters tend to view any plant as a competitor with crop trees, particularly when the trees are small. Ecologists have a contrary view. Most ecologists believe that communities are assemblages of species that don't compete much at all and coexistence is possible because species partition resource gradients differently or they avoid competition in time.

The ecologist's tool for understanding plant interactions is to measure "association" between pairs of species. The initial step is to construct for each pair of species, A and B, a contingency table that tallies for a set of NPC releves how often the species: 1) co-occurred on the same plot, 2) species A occurred but not species B, 3) species B occurred but not species A, or 4) both species were absent from the plot.

		Species B		
		present	absent	
Species A	present	a	b	a+b
	absent	c	d	c+d
		a+c	b+d	a+b+c+d=n

Our standard measure of association is Cole's Coefficient of Association (Cole 1957). We like this measure because the sign of the coefficient indicates positive or negative association and all coefficients are scaled to the range of -1 to +1. Under circumstances where joint presence indicates plant interaction, negative coefficients indicate antagonistic interaction (competition, alleleopathy), whereas positive coefficients indicate positive interaction (mutualism, symbiosis). Although Cole provides a method of calculating standard error, we chose to use traditional X^2 testing to identify statistical significance.

To calculate Cole's Coefficient of Association C_c:

1. For each species pair, arrange a 2X2 contingency table (above) such that species A occurs in fewer samples than species B. i.e. (a+b) less than or equal to (a+c).

2. Three different equations are used to calculate C_c, depending upon three mutually exclusive table conditions:

When a*d   b*c, i.e. positive association
$C_c = (a*d)-(b*c)/(a+b)*(b+d)$

When b*c   a*d and d ge a, i.e. negative association
$C_c = (a*d)-(b*c)/(a+b)*(a+c)$

When b*c   a*d and a   d, i.e. negative association
$C_c = (a*d)-(b*c)/(b+d)*(c+d)$

> *We used Cole's coefficient of association to measure pair-wise association of species in releves. The coefficient runs from -1 to +1, with the sign indicating if an association is positive or negative. Positive associations could indicate symbiosis, mutualism, or a similar response to microhabitat. Negative associations could indicate competition, allelopathy, or dissimilar response to microhabitat.*

The Cole's calculations yield an incredible number of pair-wise scores which is equal to the number of species encountered in the releves squared, divided by two minus the number of species encountered. This is far easier to envision in a symmetric table (example below) where the trace holds the trivial, perfect correlation of a plant with itself.

	ABIE15BA	ABIE69BA	ACER15RU	ACER15S2	ACER69RU	ACER69S2	ACERSPIC	ALNUINCA	ARALNUDI	ASTEMACR	ATHYANGU	BETU15PA	BETU69PA	CALACANA	..	VACCANGU
ABIE15BA	200															
ABIE69BA	200	200														
ACER15RU	133	114	200													
ACER15S2	116	84	89	200												
ACER69RU	156	111	200	105	200											
ACER69S2	200	73	142	200	120	200										
ACERSPIC	61	86	67	162	109	200	200									
ALNUINCA	80	73	56	108	58	0	139	200								
ARALNUDI	106	139	135	80	100	37	95	93	200							
ASTEMACR	0	124	129	94	121	75	104	97	112	200						
ATHYANGU	104	87	88	113	95	0	162	151	126	122	200					
BETU15PA	101	86	133	105	156	92	112	132	60	94	104	200				
BETU69PA	91	106	104	153	171	200	123	124	35	97	136	132	200			
CALACANA	44	52	49	102	48	0	100	141	82	154	125	106	116	200		
:																
VACCANGU	140	115	151	66	139	0	70	66	169	151	43	135	87	66		200

Partial table of Cole's coefficients for species pairs in FDn43 forest based upon co-occurrence in releves. Range of coefficients rescaled from –1 to 1, to 0-200 for NMS ordination. The original dataset of 50 species with >5% frequency yielded a full table of $(50^2/2)-50=1,200$ non-trivial pair-wise coefficients.

Obviously, the analysis of association matrix needs to be simplified for any practical application. First, many coefficients can be eliminated based upon statistical significance. Just limiting consideration to coefficients at the p<.05 or p<.01 levels of significance greatly reduces the pairs of interest. We used the Chi-square test to measure significance and only considered associations significant at the p<.05 level.

Also, we performed this analysis to understand how tree regeneration is affected by other plants and trees. For most of our NPC Classes, there are just a few species of commercial interest. Thus, we limited our results to just trees with fair, good, or excellent suitability (see suitability above).

Associate with White Spruce	Cole's Coefficient	Standard error
Apparently limiting		
Basswood seedlings	-1.00	0.41
Black spruce trees	-0.62	0.17
Black spruce seedlings	-0.46	0.12
Apparently beneficial		
Quaking aspen seedlings	0.15	0.07
White cedar seedlings	0.28	0.13
Thimbleberry	0.47	0.13
White spruce trees	0.56	0.11
Low-sweet blueberry	0.15	0.11

Example of Cole's coefficient of association of plants interacting with understory white spruce. All members have significant associations (p<.05) because zero is not within the standard error.

Because we were interested in how advance regeneration is affected by other plants and trees, we present only the significant (p<0.05) associations of plants with trees under 10m tall in our tables.

The standard releve plots used to sample forests in Minnesota are too large for "proper" analysis of association where we assume that jointly present species are interacting with each other. Plants can be as much as 28m apart in these releve plots. To help get around this problem, we limited the analysis to just species with mean cover-when-present over 5%. That is, the plants included were more times than not present on the releve in the 5-25% cover class or at greater cover. Our hope was that plants with at least 5-15% cover were likely interacting on the plot. This rule eliminated many plants, and more stringent rules (e.g. >10% MCWP) to assure interaction removed too many species. In scanning the initial results of understory tree association with plants, it seemed obvious that the groups of positive and negative associates were indicating a difference in local disturbance more so than competitive or mutualistic interaction. At the scale of a releve plot, it seems that the history of modest disturbance had more to do with tree establishment and that groundlayer species with similar reaction to disturbance were "brought along" in the process. To describe what might have happened, we calculated the mean synecological scores of the positive and negative associates of understory trees and looked at the difference. This tells us if a tree's establishment and recruitment – along with that of its plant associates – is likely to be favored by moister/drier, richer/poorer, warmer/cooler, or lighter/darker conditions than is "average" for that community in a mature state.

Releve plots used to sample forests in Minnesota are too large to assure plant interaction when interpreting association. Although interaction is a possible explanation for the association, it seems more likely that there are groups of co-associated understory plants that react similarly to a stand's history of disturbance. Shifts in synecological coordinates were calculated to describe differences due to disturbance and to entertain ideas as to what kinds of intermediate silvicultural treatments might have the same effect.

Analysis of association using releves was really an experiment to see what we can learn about the regenerative environment of trees. We really don't know how to interpret associations at the scale of a releve. Although we restricted our tables to just statistically significant associations, it is important to note that in communities with under 20 releves one is assured of violating the "law" of having expected values under 5 in the contingency tables. For NPCs up to about 50 releves, infrequent species still often had expected values under 5 in a cell. More study and comparison of results across all NPC Classes will help us decide if this kind of analysis has silvicultural meaning and utility.

BEWARE, when interpreting our analysis of association tables. Statistical rule have been broken in some small sample sets. Plant interaction OR disturbance can explain the associations (as can chance in small sample sets). Everything is contextual within an NPC Class, meaning that a tree's universal silvics may not match what we intepret in a particular community situation.

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Standard Releve-derived Tables for Silviculture and Forest Management

From the releve analyses, we have created a standard set of tables and figures for each wooded NPC class. Below is a summary of these standard products, followed by an example of each with an account of methods, purpose, and applications.

Table R-1, **Suitability ratings of trees**, provides a table of suitability index values for trees ranked as fair, poor, or excellent for the NPC. Also shown is the tree's presence and mean cover-when-present, which are the calculations contributing to the index. This table can be used to:
1. Select crop trees
2. Recognize and introduce missing species
3. Allow for non-commercial species
4. Recognize post-treatment success or failure
5. Anticipate competition given the choice of a crop tree

Table R-2, **Natural regeneration and recruitment of trees in mature stands**, provides a summary of how "successful" trees are as regenerants, seedlings, saplings, and trees in mature examples of the NPC. Table values are indices based upon presence and abundance, weighted by vertical complexity. Also given is the combined presence of the tree in the understory. This table can be used to:
1. Select crop trees
2. Recognize and introduce missing species
3. Allow for non-commercial species
4. Recognize post-treatment success or failure
5. Anticipate competition given the choice of a crop tree

Table R-3, **Association of tree regeneration with overstory trees, understory trees, shrubs, and common herbs**, provides a summary of species that have a positive or negative association with understory trees for the NPC. Table values are Cole's Coefficient of Association as a measure of the strength of association. Also shown are the raw counts of coincidence of a tree's regeneration with its parent tree. Shifts in synecological coordinates are provided for the groups of species with positive and negative association with understory trees. This table can be used to:
1. Understand how the presence or absence of seed trees affects regeneration potential.
2. Identify species that may enhance or inhibit the development of advance regeneration. (i.e., using the current vegetation to predict population changes in tree regeneration)
3. Design silvicultural treatments to encourage or discourage regeneration of particular species.

(Example R-1) Suitability Index of Trees on MHn35 Sites

The index of suitability is our estimate of a tree's ability to compete with all plants on MHn35 sites without silvicultural assistance. The raw index is based upon the product of percent presence and mean cover-when-present (below) within the set of MHn35 releves in mature, natural stands. Plants are ranked by their raw index and the full range re-scaled to run from zero to five to yield the suitability index (below). The re-scaling is done so that whole numbers represent 20-percentile classes: excellent=80-100; good 60-80; fair=40-60; poor=20-40; N/A=0-20.

Tree	Presence as Tree	Mean Cover When Present	Suitability Index*
Sugar maple (Acer saccharum)	81%	32%	5.0
Basswood (Tilia americana)	65%	15%	4.8
Northern red oak (Quercus rubra)	49%	20%	4.7
Paper birch (Betula papyrifera)	61%	13%	4.6
Quaking aspen (Populus tremuloides)	31%	20%	4.4
Red maple (Acer rubrum)	31%	12%	4.1
Big-toothed aspen (Populus grandidentata)	13%	19%	3.7
Ironwood (Ostrya virginiana)	24%	8%	3.4
White pine (Pinus strobus)	7%	24%	3.1
Bur oak (Quercus macrocarpa)	11%	10%	2.5
Yellow birch (Betula alleghaniensis)	10%	9%	2.2
Balsam fir (Abies balsamea)	8%	8%	2.0
*Suitability rankings: **excellent**, **good**, **fair**			

R-1, Brief Methods

For this analysis we created a very simple index to estimate suitability. This index is the product of percent presence and percent cover when present. For example, there are 256 sample plots of Northern Mesic Hardwood Forest (MHn35). Basswood trees over ten meters tall (~33 feet) occur in 164 of these plots, thus its percent presence as a tree is (164/256)*100= 64.1%. The mean cover of basswood trees on those 164 plots is 15.0%. Thus, its index is 64.1*15.0=962.

To communicate our estimates of suitability, we ranked the indices of plants that often occur (>5% presence) in a community and divided that ranking into 5 equal parts to create five suitability classes: excellent, good, fair, poor, and not suitable. Continuing the example above, 113 plants were ranked for MHn35 and basswood had the 8th highest ranking, placing it in the excellent class along with 22 other plants with the highest index values.

Because communities have different numbers of plants with >5% presence and because their ranges of index values are different, we calculated a scaled index for comparisons among communities for each tree. The scaling represents a tree's rank order on a scale of 0-5, so that the integer of the scaling indicates its suitability class (e.g., 4.xx is in the excellent class, 3.xx is in the good class, etc.). The scaled index=(proportion of plants with lower ranking)/20.

Nearly all of the data used to calculate the suitability index come from stands near the mid-point of normal stand development (40-80 years). Suitability is expected to change throughout succession, depending upon a tree's seral status: early-, late-, or mid-successional. This table is the best that can be constructed, given the paucity of releve samples in very young and very old forests.

The table is not intended to take precedence over current stand conditions. There is no better evidence that a tree can grow well and reach commercial stocking levels than the observation that it is currently doing so.

R-1, Silvicultural Applications

1. **Select crop trees**
   a. In general, trees with higher suitability indices are better choices as crop trees than trees with lower indices.
   b. If stands are to be silviculturally manipulated to favor one species over another, mean-cover-when-present is the more important element of the index, with the higher covers predictive of the likelihood of higher stocking.
2. **Recognize and introduce missing species**
   a. Species with a high suitability index that are not currently present on the site can be introduced to the site with less risk than species with a lower index.
3. **Allow for non-commercial species**
   a. Trees with an excellent, good, or fair rating should be allowed at modest abundance when they have a species-specific attribute that makes them desirable for purposes other than timber production
4. **Quantify post-treatment success or failure**
   a. The table offers a means of measuring success by species groups (e.g. Treatment is expected to achieve a minimum of 80% stocking of excellent-ranked species at 5 years.)
5. **Anticipate competition given the choice of a crop tree**
   a. Species with a higher suitability index than the chosen crop tree are more likely to be competitors that need control in order to favor the crop tree.
   b. Species with a lower suitability index than the chosen crop tree are more likely to be subordinates (unless at high abundance) that shouldn't interfere with the regeneration and growth of the crop tree.

(Example R-2) **Natural Regeneration and Recruitment of Trees in Mature MHn35 Stands**

Table values are natural regeneration indices for regenerants (<10cm tall), seedlings (10cm-2m), saplings (2-10m), and trees (>10m) in MHn35 forests. Index ratings express our interpretation of how successful tree species are in each stratum compared to other trees in MHn35 communities. All indices equally weight percent presence, mean cover when present, and mean number of reported strata – the raw index being the product of these numbers. Trees are ranked by their raw index and the full range re-scaled to run from zero to five to yield the R-, SE-, SA-, or T-index (below). Re-scaling is done so that whole numbers represent 20-percentile classes: excellent=80-100; good 60-80; fair=40-60; poor=20-40; N/A=0-20. Also shown is the combined percent presence of trees in the understory strata (R, SE, SA) to provide an estimate of how often one encounters advance regeneration of that species in MHn35 forests.

Tree	Presence R, SE, SA	R-index	SE-index	SA-index	T-index
Sugar maple (Acer saccharum)	96%	5.0	5.0	5.0	5.0
Ironwood (Ostrya virginiana)	83%	4.8	4.8	4.8	3.0
Northern red oak (Quercus rubra)	80%	4.2	4.0	3.3	4.3
Basswood (Tilia americana)	80%	4.5	4.3	4.5	4.5
Red maple (Acer rubrum)	64%	4.3	4.2	3.8	3.8
Balsam fir (Abies balsamea)	51%	3.7	3.5	2.5	2.3
Quaking aspen (Populus tremuloides)	47%	3.7	3.3	2.7	4.0
Paper birch (Betula papyrifera)	39%	1.7	1.3	3.2	4.5
Bur oak (Quercus macrocarpa)	17%	2.2	1.7	2.3	2.8
Big-toothed aspen (Populus grandidentata)	11%	1.8	1.5	1.8	3.8
White pine (Pinus strobus)	10%	2.7	2.3	1.5	3.3
Yellow birch (Betula alleghaniensis)	10%	1.3	1.3	2.5	3.0
Index ratings: **Excellent**, **Good**, **Fair**, Poor, N/A					

R-2, Methods*

The releve method of sampling forest vegetation describes explicitly how trees occur at different heights. We modified raw releve samples by interpreting the occurrence and cover of trees in four standard height strata: regenerants 0-10cm tall, seedlings 10cm-2m tall, saplings 2-10m tall, and trees taller than 10m. The releve samples all come from forests with an established canopy, so this dataset documents the presence and cover of trees in strata that have formed during the process of stand maturation (i.e., understory development).

We created an index to measure roughly the regenerative success of a tree in each stratum. The index is the product of (1) percent presence in that stratum for all releves classified as that community, (2) mean percent cover of that species when present in a stratum, and (3) the mean number of different strata reported in the releves when that species is present. The indices for all trees were ranked, the range was then scaled to range between zero and 5. The index ratings of excellent, good, fair, poor, and not-applicable are the 5 whole number segments of the index.

*The tree index in table R-2 is not the same calculation or ranking as the suitability index of table R-1.

R-2, Silvicultural Applications

1. **Estimate the overall ability of the community to develop silviculturally significant advance regeneration**
   a. In general, trees with excellent-to-good R-, SE-, and SA-indices can be depended upon to produce enough advance regeneration to stock a stand after removal of canopy trees
   b. In general, the number of native trees with excellent-to-good R-, SE-, and SA-indices is correlated with the community's historic dependence upon fine-scale or catastrophic disturbance for regeneration. High numbers of trees are correlated with fine-scale disturbance dynamics and long rotations of catastrophic disturbance. Low numbers of trees are correlated with coarse-scale disturbance dynamics and short rotations of catastrophic disturbance.

2. **Estimate seedbed suitability or sprouting ability of trees under the canopy of a mature forest and on an undisturbed forest floor.**
   a. In general, trees with excellent-to-good R-index will not require seedbed preparation.
   b. In general, trees with good-to-fair R-index will most likely require seedbed preparation that mixes the organic layer into the mineral soil.
   c. In general, trees with a poor R-index will most likely require seedbed preparation that bares mineral soil.

3. **Estimate the shade tolerance of trees under the canopy of a mature forest**
   a. In general, trees with excellent-to-good SE- and SA-index are considered to be shade tolerant and able to recruit into the canopy using small, single-to-few tree gaps.
   b. Conversely, trees with fair-to-poor SE- and SA-index are considered to be shade-intolerant and recruit into the canopy only in rather large gaps or in the open.

4. **Identify recruitment bottlenecks**
   a. In general, the lowest index among the four (R-, SE-, SA-, T-) indicates the height-class where that tree has the greatest trouble recruiting given the "usual" conditions in mature forests.
   b. Experience with this table suggests that relative declines or dips among the indices need to be about a whole unit to be "significant," meaning that a recruitment problem identified in the table is commonly observed by field foresters familiar with the community.
   c. The absolute values are important, meaning that bottlenecks from excellent to good, present far less a silvicultural obstacle than dips from fair to poor.

(Example R-3) Association of tree regeneration with overstory trees, understory trees, shrubs, and common herbs in MHn35 forests (partial table for illustration)

This table presents information concerning how seedlings and saplings (< 33' tall) of MHn35 trees associate with other forest plants including their own trees. Coles' coefficient of association (CC) was used to measure the degree and nature of association. The coefficient ranges from -1 (strongly negative) to +1 (strongly positive). All associations in the table are statistically significant (P<0.05). Shown in the leftmost column are the raw counts from 578 MHn35 releve plots used to calculate CC between advance regeneration and its parent tree: U&T, joint presence in canopy and understory; U only, regeneration present but trees absent; T only, trees present but not regeneration; neither, joint absence. The last row of each species block lists the environmental situations that might have favored the positive or negative guilds. This was estimated by calculating the shift in mean synecological scores between the negative associates versus positive associates regarding moisture, nutrients, heat, and light. Shifts greater than a whole synecological unit are in bold text, and the greatest shift indicated by an asterisk.

Understory Tree	Positive associates				Negative Associates			
	Overstory	CC	Understory	CC	Overstory	CC	Understory	CC
Balsam Fir	Balsam fir	0.94	Yellow birch	0.61	Quaking aspen	-0.19	Leatherwood	-0.11
U & T: 65	Yellow birch	0.49	Long-stalked sedge	0.24	Northern red oak	-0.21	Quaking aspen	-0.12
U only: 241	Red maple	0.17	Beaked hazelnut	0.20			Hog peanut	-0.17
T only: 2			Mountain maple	0.17			Early meadow-rue	-0.27
Neither: 270			Lady fern	0.11			Lrg-flrd bellwort	-0.36
CC= +0.94							Rnd-lvd dogwood	-0.38
	Moister*, poorer, cooler, darker favors balsam fir				Drier*, richer, warmer, lighter inhibits balsam fir			
Red Maple	Red maple	0.87	Interrupted fern	0.48	Basswood	-0.14	Ironwood	-0.18
U & T: 160	Balsam fir	0.35	Bracken	0.36	Sugar maple	-0.29	Basswood	-0.21
U only: 180	Northern red oak	0.13	Beaked hazelnut	0.26			Leatherwood	-0.25
T only: 2	Paper birch	0.08	Tall blackberry	0.22			Lrg-flrd bellwort	-0.46
Neither: 229			Pale bellwort	0.20			Sugar maple	-0.62
CC= +0.87			Northern red oak	0.16				
			Quaking aspen	0.12				
			Mountain maple	0.12				
	Moister, **poorer***, cooler, **lighter*** favors red maple				Drier, **richer***, warmer, **darker*** inhibits red maple			
Sugar Maple	Sugar maple	0.93	Leatherwood	0.72	Balsam fir	-0.14	Rnd-lvd dogwood	-0.24
U & T: 442	Northern red oak	0.73	Ironwood	0.48	Bur oak	-0.24	Bur oak	-0.32
U only: 98			Northern red oak	0.35	Quaking aspen	-0.41	Tall blackberry	-0.37
T only: 2			Basswood	0.18			Early meadow-rue	-0.38
Neither: 36							Bracken	-0.42
CC= +0.93							Red maple	-0.62
							Quaking aspen	-0.63
							Beaked hazelnut	-0.86
	Moister, **richer***, warmer, **darker** favors sugar maple				Drier, **poorer***, cooler, **lighter** inhibits sugar maple			
Yellow Birch	Sugar maple	0.80	Northern red oak	0.75	Quaking aspen	-0.80	Lrg-flrd bellwort	-0.16
U & T: 32	Yellow birch	0.70	Balsam fir	0.61	Big-toothed aspen	-0.81	Wild sarsaparilla	-0.17
U only: 12	Ironwood	0.18	Lady fern	0.36			Early meadow-rue	-0.44
T only: 14			Interrupted fern	0.16			Bracken	-0.45
Neither: 520							Tall blackberry	-0.53
CC= +0.70							Quaking aspen	-0.54
							Rnd-lvd dogwood	-1.00
	Moister, richer*, warmer, darker favors yellow birch				Drier, poorer*, cooler, lighter inhibits yellow birch			

R-3, Brief Methods

We used Cole's coefficient of association to calculate the degree of association between the regeneration of tree species (seedlings and saplings <10m tall) and plants that might interact with regeneration such as the canopy trees and plants that co-occur on a 20X20m releve plot. Only plants with 10% presence and 5% mean cover-when-present were used because we wanted to focus on species that foresters are likely to encounter and on species with high abundance capable of competing with or enhancing advance regeneration. The initial step is to construct a 4-cell contingency table that sums the possible co-occurrence conditions for a species pair: a=both species on the plot; b=one species without the other; c=the other species only; d=both species absent. Higher than expected values of joint occurrence and joint absence (a & d) indicate positive association. Higher than expected values of one species occurring without the other (b & c) indicate negative association. The formulae used to calculate the coefficient assure that the results range from -1 to + 1, with the negative values indicating the strength of negative association and positive values indicating the strength of positive association. Because this is a standard contingency table, Chi-square methods can be used to test for statistical significance.

In the leftmost column of the table, we present the actual raw counts of the co-occurrence of tree regeneration with its parent tree. Using balsam fir as an example: a=U&T, meaning that balsam fir regeneration and balsam fir trees jointly occurred in 65 releves of the 578 MHn35 releve plot set; b=U only, meaning that there were 241 releves with fir regeneration but not fir trees; c=T only, meaning that fir trees occurred on 2 plots without any fir regeneration; d=Neither, meaning that no fir occurred on 270 plots. We present raw counts, rather than percents so that one can get a general feeling for how common it is for advance regeneration of that species to be present in MHn35 forests. For balsam fir, its presence=(a+b)/578=(65+241)/578=53%. (Note: presence calculated this way will not exactly match presence values in Table R-2 because the releve dataset has grown since Table R-2 was constructed.

For regeneration of each tree species, we separated the associated species by their presence in the canopy and whether they were positive or negative associations to yield four species columns. The table holds only species with significant (P<0.05) association. The species are ranked so that those with the strongest associations (largest departures from zero) are in the top row.

For small plots, significant associations are usually interpreted as plant interaction: competition, mutualism, symbiosis, allelopathy, etc. Small plots are generally used to assure that the plants are competing for growing space or are close enough to chemically influence one another. Our 20X20m releve plots are not small enough to assure such interaction. We attempted to correct this by including plants with at least 5% mean cover-when-present, but there is no guarantee that joint occurrence means interaction. We believe that significant association likely relates to disturbance history on large plots. Thus, the positive and negative groups are viewed as species guilds that react to disturbance similarly – the regeneration of the tree species in question being a member of one guild and not the other. In most cases, one group of associates comprises species that are more ruderal than those in the other group. In general, the ruderal group is a positive associate of early successional trees and the negative group is an associate of mid- or late-successional trees. Doing nothing should favor continued development of regeneration associated with the non-ruderal guild. Silvicultural treatment that emulates natural disturbance should favor development of regeneration associated with the ruderal guild – but what kind of disturbance?

To guess at the kind of disturbance that needs to be emulated or avoided, we calculated the mean synecological coordinates of both the ruderal guild and non-ruderal guild. This was done with all species, not just those showing significant association. By calculating the difference in coordinates of the two guilds, we can at least guess if regeneration would be favored or disfavored by shifts to moister/drier, richer/poorer, warmer/cooler, or lighter/darker environmental conditions. The art of improving advance regeneration of a crop tree would then be to match silvicultural systems or treatments to the beneficial constellation of coordinate shifts. The table lists all of the complementary shift trends, with large departures (shifts >1 synecological unit) indicated by bold text.

R-3, Silvicultural Applications

1. **Understand how the presence or absence of seed trees affects regeneration potential**
   a. In general, regeneration with comparatively high joint occurrence and joint absence with their trees (high positive CC) are late-successional species with excellent seedling bank potential.
   b. In general, regeneration with comparatively high U-only counts are species able to develop significant advance regeneration from very few seed (or suckering) trees.
   c. In general, species with comparatively high T-only counts are species that do poorly in mature forests and require silvicultural intervention to build adequate advance regeneration.
2. **Identify species that may enhance or inhibit the development of advance regeneration. (i.e. using the current vegetation to predict population changes in tree regeneration)**
   a. In general, high cover of negative overstory associates in a particular stand would need to be removed to some degree in order to enhance regeneration.
   b. In general, high cover of negative understory associates in a particular stand diminish expectations of adequate regeneration, whether natural, seeded, or planted.
   c. In general, high cover of positive overstory associates in a particular stand increase expectation of regeneration and those trees are good choices as a cover or shelter for regeneration, whether natural, seeded, or underplanted.
   d. In general, high cover of positive understory associates in a particular stand increase expectations of adequate regeneration, whether natural, seeded, or planted.
3. **Design silvicultural treatments to encourage or discourage regeneration of particular species**
   a. In general, silvicultural treatments affect site moisture by: compaction, rutting, residual duff thickness and continuity, residual coarse woody debris, canopy retention, and transpiration potential of residual plants.
   b. In general, silvicultural treatments affect site nutrients by: removal, changing the amount and kind of detrital food available to microbes, the abundance and diameter distribution of woody debris, and conversion to species with richer or poorer litter.
   c. In general silvicultural treatments affect site heat (longer wavelength radiation) and light (shorter wavelength radiation) by: canopy removal or simplification, residual duff thickness and continuity, changing reflectance of the ground surface, and conversion to trees with different architecture and accessory pigments.
   d. The magnitude and sometimes even direction of a factor's effect on moisture, nutrients, heat, and light (a-c above) depends upon the NPC class, soil texture, topography, and site hydrology.
   e. Synecological coordinates are partially correlated and it is not always possible to design a treatment that will move all four coordinates in the directions needed.