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A shade tolerance index for common understory species of northeastern North America

Lionel Humbert *, Daniel Gagnon, Daniel Kneeshaw, Christian Messier

Groupe de Recherche en Écologie Forestière Interuniversitaire (GREFi), Département des Sciences Biologiques, Université du Québec à Montréal, Case Postale 8888, Succursale Centre-Ville, Montréal, Qc., Canada H3C 3P8

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Abstract

Since Baker's [Baker, F.S., 1949. A revised tolerance table. J. For. 47, 179–181] classic contribution, shade tolerance indices have not been much modified for North American plant species. While many common tree and shrub species are included in the shade tolerance index, much less is known about this characteristic for the abundant and rich understory vascular and nonvascular plant layers. The classification of the shade tolerance is widely used to compare relative growth and survival among plant species under closed canopies and is also fundamental to an understanding of stand development following small and large scale disturbances. Although qualitative, it is frequently used both in research and management implications. Here we provide a significant revision to Baker's shade tolerance table to include the most common forest understory plant species found in northeastern North America forests. Our index is based on: (1) the compilation of the opinions of five experts, (2) a comparison with Ellenberg's index from Europe as well as, (3) information from current literature. For most of the 347 plant species investigated, a consistent and robust shade tolerance index, ranging between 1 (very tolerant) and 9 (very intolerant), was found. Here we present revised shade indices for 71 tree and shrub species, 185 herbaceous species, and 91 bryophyte and lichen species.

Keywords: Shade tolerance; Understory species; Ellenberg L index; Baker shade tolerance table

1. Introduction

Light is one of the most studied ecological factors in plant ecophysiology due to its essential function autotrophic plants. It has been characterized under a wide variety of atmospheric conditions and under various plant covers (e.g. Hutchison and Matt, 1977; Gendron et al., 1998). We now know that not only its quantity, but also its quality and variability are important characteristics for plant growth. Similarly, many basic characteristics of plant functional acclimatation and adaptation to light have been reported (Messier et al., 1999). However, even with our extensive documentation of the range of light conditions, the fundamental mechanisms of shade tolerance are still not fully understood (Lin et al., 2001). What we know is

* Corresponding author. Tel.: +1 514 9873000.
E-mail address: humbert.lionel@courrier.uqam.ca (L. Humbert).

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that shade tolerance includes a suite of traits that can take different forms depending on the species and the environments. However, generally, shade tolerance indicates the degree to which a plant can survive and grow in low light conditions (Shirley, 1943; Kobe et al., 1995), and plants have been classified into three broad categories: shade tolerant, intermediately shade tolerant and shade intolerant species (Anderson et al., 1969). Although imperfect and rather coarse, such a classification has proven very useful in classifying trees into broad functional types (Baker, 1949).

However, useful such a classification has been for tree and shrub species, there is no North American equivalent for understory herbaceous plants, bryophytes and lichens. In Europe, Ellenberg (c.f. Ellenberg, 1979; Ellenberg et al., 1992) has successfully characterized the shade tolerance of most plants using an index from 1 to 9. This classification has proven to be very useful not only to better understand the autecology of plant species, but also to use the presence or absence of various understory plant species as an indicator of understory light levels.

This paper proposes a shade tolerance index of common understory species present in the temperate hardwood forest of southern Quebec, Canada, and, in fact, common in northeastern North America.

2. Methods

An index of shade tolerance was developed for common forest understory species where shade tolerance was based on three independent sources of information. First, a group of five experts was surveyed and asked to rank the shade tolerance of a number of plant species (see below). Secondly, these responses were validated with published information available for understory species, mostly studied in North America. Thirdly, these results were compared with the ranking proposed by Ellenberg in Europe for co-occurring species.

2.1. Using the opinions of experts

As with Baker (1949) and, more recently, Hess and King (2002), a questionnaire was sent to five expert plant ecologists who have extensive field experience with most plants found in the northeastern North American forest. The list included close to 400 species, including bryophytes and lichens. For woody species, only the seedling stage was considered.

The questionnaire required respondents to rank the light environment where the species grow and survive most commonly on a scale of one to five. The five levels were: (1) deep shade, (2) shade, (3) moderate shade, (4) partly open and (5) completely open. No indications of the light environment (percent of full sunlight) was required or requested. Due to the nature of the question, the answers did not provide a direct shade tolerance ranking, but rather an evaluation of the overall light environment in which the species were found to grow well. According to Brissot (1972), the light environment is the sum of three environmental factors: light, temperature and desiccation. In addition, the common occurrence of a species at a particular light level does not mean that this species is at its physiological optimum, but only that it is the best competitor in this environment. Consequently, we have determined the ‘‘ecological existence’’ not the ‘‘ecological potential’’ (Ellenberg, 1996; Whittaker et al., 1973) of each plant species at a given light level.

All results were then adjusted to a nine level scale for comparisons with Ellenberg’s index. This transformation did not change the mean of the values; consequently, comparisons between data were not affected. An overall result was compiled from the questionnaires and the mean ($\bar{X}_e$) and standard deviation (σ_e) were calculated.

2.2. Using published data

Published results have focused primarily on the response of tree species, rarely are herbaceous species and bryophytes reported in shade tolerance studies. In this paper, the following references were used: Grandtner (1997), Burns and Honkala (1990a, b), Minnesota Department of Transportation (2002), Ritchie (1996), Bakuzis and Hansen (1959), Haussler and Coates (1986), Beaudry et al. (1999), Jobidon (1995), Ellenberg et al. (1992). The publication by Ellenberg et al. (1992) is important because of the vast number of species described and the strong correspondence between bryophytes in Europe and North America, as well as of some introduced vascular plants. The Ellenberg L index is based on phyto-sociological relevés combined with light measurements taken during the summer. Nearly 140 species, of which half are bryophytes, are present in both Quebec and Europe and could then be compared.

As with the previous section for the experts, all results were then adjusted to a nine level scale, the mean ($\bar{X}_p$) and the standard deviation (σ_p) were calculated.

2.3. Compilation

We chose to compile these data into a synthetical index based on the comparison of the mean and the standard deviation of the different sources. The kind of system used here is a hierarchical one which allows us to automatize the ranking, and the different levels in the hierarchy are used to optimize the usefulness of the data. We first classified results into two categories : homogeneous and nonhomogeneous, and this is done for the expert part of the data and the published part. This homogeneity is simply related to σ. When both expert and published data were homogeneous we compared means, and if the difference was no more than two, we used the expert result as the index. If not, this result was rejected and a second level of integration was conducted. This second level mixed together expert and published data. To do this we calculated σ, and as in the upper level (explained above) we deduced the homogeneity from it. When it was homogeneous, we took the $\bar{X}$ as the index. Rejected results were analysed in a final level case by case. When the general result was close (one or two points higher or lower) to the Ellenberg index we systematically chose the Ellenberg index. This choice was driven by the fact that Ellenberg's index is more precise (nine levels) compared to our questionnaire (five levels).

3. Results and discussion

3.1. Questionnaire and data from the literature

Table 1 shows a compilation of the classification given by the five experts. At least one expert evaluated all woody species, both tree seedlings and shrubs. The family Salicaceae and the genus *Amelanchier* received the fewest responses. We received responses for nearly all the herbaceous species included in the survey. Only five species (2%) could not be evaluated by any of the experts. An additional 23 species (11%) received evaluations from only one expert. Among herbaceous plants, the Poaceae and Renonculaceae families received the fewest responses. Among the bryophytes, however, the response level was much lower, with no responses being provided for 74 species and only one answer for 34 other species.

Table 1
Comparison between the original list of species, collected data and the resulting number of species with an attributed shade tolerant index value

	Total species	Trees and shrubs	Herbaceous plants	Bryophytes and lichens
Original list	405	72	201	132
Botanist A	96	42	48	6
Botanist B	239	67	141	31
Botanist C	223	47	151	25
Botanist D	291	71	187	33
Botanist E	172	53	119	0
Published	128	57	57	14
Ellenberg	139	3	50	86
Synthetic index	347	71	185	91

The responses of the experts (Table 2) are very similar for 48% of the species and can be qualified as homogeneous. This homogeneity is defined by a low σ, in this case less than 1.75, 1.50, 1.25 and 1.00 depending on the number of responses. For 16% of the species, the responses of the experts are different ($\sigma_e > 2.25$), for 6% of the species the responses are very different ($\sigma_e > 3.00$).

From the literature reviewed, data was obtained for 128 species (57 woody species, 57 herbaceous species, and 14 bryophytes and lichens) (Table 1). However, 76 of these species (59%) were found in only one publication. Similar to the questionnaire, information from literature (Table 2) was homogeneous for 28% of the species, different for 4%, and very different for one species. In light of this variation, results from the experts and the literature were compared to produce a synthetic index (Column I in Table 2).

3.2. Comparisons

Comparisons between the published data and the expert opinions show a difference greater or equal to three light levels for 19 species. Eight of these are

Table 2
Shade tolerance index for common understory species in the temperate hardwood forest of southern Quebec

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Achillea millefolium	H	€	4	0	9	3	1.15	7.7	8	8
Actaea pachypoda	H		3	1.53	2.7					3
Actaea rubra	H		4	1.26	2.8	2	0	3		3
Adiantum pedatum	H		4	1	2.5					2
Ageratina altissima	H		3	1	6					6
Agrimonia gryposepala	H		2	3.54	5.5					X
Agrimonia striata	H		2	4.24	6					X
Agrostis capillaries	H	€	2	0	9	2	1.41	8	7	9
Agrostis gigantean	H	€	1		9				7	7
Anaphalis margaritacea	H		4	1	8.5					9
Anemone canadensis	H		3	1	8	1		7		8
Anemone virginiana var. *alba*	H		1		8					8
Antennaria parlinii ssp. *fallax*	H		1		9					9
Apocynum androsaemifolium	H		5	0.89	8.6	1		7		9
Aquilegia canadensis	H		2	0.71	8.5					8
Arabis drummondii	H		2	0	9					9
Aralia nudicaulis	H		5	1.67	4.6	1		3		5
Asplenium viride	H		4	3.65	5				4	4
Aster puniceus	H		4	2.58	6					X
Athyrium filix-femina	H		5	1.67	3.4	4	0.96	1.8	3	3
Botrychium virginianum	H		4	0	3				6	3
Calamagrostis canadensis	H		4	0	9	1		6		9
Calypso bulbosa	H		3	1.15	1.7					2
Cardamine diphylla	H		3	0.58	2.7					3
Carex arctata	H		4	1.71	3.3					3
Carex brunnescens	H		1		4				9	9
Carex communis	H		2	0.71	3.5					4
Carex deweyana	H		2	0.71	3.5					4
Carex intumescens	H		4	1.89	4.3					3
Carex pensylvanica	H		1		8	1		3		X
Carex retrorsa	H		1		9					9
Carex trisperma	H		2	1.41	6					6
Centaurea nigra	H	€	1		9	1		7	8	8
Chimaphila umbellate	H		4	0.96	3.8				4	4
Chrysosplenium americanum	H		2	1.41	4					4
Cinna latifolia	H		3	3.06	5.7	1		3		X
Circaea alpina	H		4	0.5	2.8	1		1	4	4
Cirsium muticum	H		3	1.15	7.7					8
Claytonia caroliniana	H		4	1	8.5					9
Clinopodium vulgare	H		2	2.83	7	1		7	7	7
Clintonia borealis	H		5	0.89	3.6					4
Coeloglossum viride var. *virescens*	H		2	0	3					3
Comandra umbellate ssp. *umbellate*	H		3	3.21	6.7					X
Conioselinum chinense	H		3	2.65	4					X
Coptis trifolia	H		5	0.45	3.2					3
Corallorhiza maculata	H		4	1	1.5					1
Corallorhiza trifida	H		5	1.67	2.6				x	3
Cryptogramma stelleri	H		2	2.83	5					X
Cypripedium acaule	H		4	1.89	4.3					3
Cystopteris bulbifera	H		3	1.53	3.3	1		3		3
Cystopteris fragilis	H		3	1	4				5	5
Danthonia spicata	H		3	2.31	7.7					9

Table 2 (*Continued*)

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Deschampsia flexuosa	H		2	0	9	1		7	6	9
Dicentra cucullaria	H		3	3.46	7					X
Draba arabisans	H		2	1.41	8					8
Drosera rotundifolia	H		4	1	8.5				8	8
Dryopteris carthusiana	H		5	1.1	2.8				5	3
Dryopteris marginalis	H		4	2.22	3.8					X
Elymus trachycaulus ssp. *trachycaulus*	H		2	1.41	8	1		7		8
Empetrum nigrum	H		4	0	9	1		7	7	9
Epigaea repens	H		4	2.31	5					X
Epilobium angustifolium	H		5	0	9	5	0.89	7.6	8	8
Epilobium ciliatum ssp. *glandulosum*	H	$	3	1.15	8.3					8
Epilobium palustre	H		3	2	7				7	7
Equisetum arvense	H		4	2.75	5.8	1		7	6	6
Equisetum hyemale	H		4	2.22	6.3	1		3	5	5
Equisetum pratense	H		3	2.65	6				5	5
Equisetum scirpoides	H		3	0.58	2.7					3
Equisetum sylvaticum	H		5	0.89	3.6	1		3	3	3
Eriophorum virginicum	H		4	0	9					9
Eupatorium maculatum	H		4	1	8.5	1		7		9
Eurybia macrophylla	H		4	1.63	5					6
Fragaria virginiana	H		5	0.89	8.6	1		5		9
Galeopsis tetrahit	H	€	5	1.1	8.2	1		9	7	7
Galium asprellum	H		5	2.61	5.4					X
Galium trifolium	H		5	2.19	3.6	1		3		X
Gaultheria hispidula	H		5	2.24	4	1		3		3
Gaultheria procumbens	H		5	2.19	5.4					X
Geum rivale	H		3	1.15	5.7	1		7	6	6
Glyceria striata	H		3	2	7				7	7
Goodyera oblongifolia	H		3	0	1	1		3		1
Goodyera repens	H		4	1.15	2	1		5		2
Gymnocarpium disjunctum	H		4	1.26	2.8					3
Heracleum sphondylium ssp. *montanum*	H		4	1	8.5	1		7	7	7
Hieracium caespitosum	H	€	3	0	9				8	8
Hieracium scabrum	H		3	1.15	8.3					8
Huperzia lucidula	H		5	0.89	2.6					3
Hypericum perforatum	H	€	4	1	8.5	1		8	7	7
Impatiens capensis	H		4	2.22	3.8					X
Iris versicolor	H		5	1.67	7.6					8
Lactuca biennis	H		4	2	8					9
Lactuca canadensis	H		2	0	9					9
Leucanthemum vulgare	H	€	4	0	9					9
Linnaea borealis	H		5	2.28	3.8				5	5
Listera convallarioides	H		4	1.63	3					3
Listera cordata	H		4	1.63	3				3	3
Lycopodium annotinum	H		5	0.89	4.4				3	3
Lycopodium clavatum	H		4	2.22	5.8				8	8
Lycopodium complanatum	H		4	1	4.5					5
Lycopodium obscurum	H		5	0.45	3.2					3
Lycopodium tristachyum	H		4	1.26	5.3					5
Maianthemum canadense	H		5	1.79	3.8	2	0	3		4
Maianthemum trifolium	H		4	1.91	7.5					8
Matteuccia struthiopteris	H		4	2.06	4.8				5	5
Medeola virginiana	H		4	1.26	2.8					3

Table 2 (*Continued*)

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Melampyrum lineare	H		4	1.5	5.8	1		3		5
Mentha arvensis	H		2	0.71	8.5	1		7	6	8
Mentha canadensis	H		2	0.71	8.5					8
Milium effusum	H		3	3.46	5	1		3	4	4
Mitchella repens	H		4	1.26	2.8					3
Mitella nuda	H		5	0.89	2.4					2
Moneses uniflora	H		4	0.96	2.3				4	4
Monotropa hypopithys	H		4	0.96	1.8	1		3		2
Monotropa uniflora	H		5	0.45	1.2	1		3		1
Onoclea sensibilis	H		5	1.79	5.2	1		3		5
Orthilia secunda	H		3	1	2	2	0	3	4	2
Oryzopsis asperifolia	H		4	1.5	4.3					4
Oryzopsis pungens	H		2	3.54	5.5					X
Osmorhiza berteroi	H		3	1.53	2.7					3
Osmorhiza longistylis	H		3	1.53	2.7					3
Osmunda cinnamomea	H		5	2.97	5.4	1		3		X
Osmunda claytoniana	H		4	2.22	4.3					5
Oxalis acetosella	H		4	1.63	3	1		1	1	1
Panicum acuminatum var. *acuminatum*	H		2	0	9					9
Pedicularis canadensis	H		2	4.24	4					X
Petasites frigidus var. *palmatus*	H		4	3.46	6	1		2		X
Phegopteris connectilis	H		4	1.26	2.8					3
Platanthera dilatata var. *dilatata*	H		2	2.83	5					X
Platanthera obtusata	H		3	1.15	3.7					4
Platanthera orbiculata	H		3		3	1		3		3
Poa interior	H		1		9					9
Polygala paucifolia	H		4	3.3	4.8					X
Polygonatum pubescens	H		4	2.5	3.8					X
Polypodium virginianum	H		4	1.26	2.8	1		3		3
Polystichum braunii	H		4	1.63	3				3	3
Polystichum lonchitis	H		3	0	3				6	3
Potentilla norvegica	H		4	1	8.5				7	7
Potentilla recta	H	€	1		9				9	9
Potentilla simplex	H		1		9					9
Prenanthes altissima	H		4	3.4	4.3					X
Prenanthes trifoliolata	H		3	1.53	2.7					3
Prunella vulgaris	H		4	3.46	6	1		9	7	7
Pteridium aquilinum	H		3	1.15	7.7	3	1.73	6	6	6
Pteridium aquilinum var. *latiusculum*	H		4	1.63	7	2	2.83	5		7
Pyrola asarifolia	H		4	0.5	2.8					3
Pyrola chlorantha	H		3	1.15	3.7	1		5		4
Pyrola elliptica	H		5	0.89	3.6					4
Pyrola rotundifolia	H		5	1	4	1		3	4	4
Ranunculus abortivus	H		3	1.15	6.3					6
Ranunculus acris	H	€	3	0	9				7	9
Ranunculus repens	H	€	2	2.83	7	1		5	6	6
Rubus allengheniensis	H		2	0	9					9
Rubus chamaemorus	H		4	1.15	8				9	9
Rubus idaeus	H		5	0.89	8.4	5	1.1	7.2	7	7
Rubus pubescens	H		5	1.67	3.4					3
Rumex aquaticus var. *fenestratus*	H		2	0	9					9
Sanguisorba canadensis	H		4	1	8.5	1		3		9
Sanicula marilandica	H		3	2.52	3.3					4

Table 2 (*Continued*)

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Saxifraga paniculata ssp. *neogaea*	H		4	0	9					9
Schizachne purpurascens	H		3	2.31	7.7	1		5		9
Scutellaria lateriflora	H		4	2.06	5.3					X
Senecio aureus	H		1		9					9
Smilacina racemosa	H		4	1.89	4.3					3
Solidago hispida	H		3	2	7					6
Solidago juncea	H		1		9					9
Solidago macrophylla	H		4	3	5.5					X
Solidago rugosa	H		4	1.63	7					7
Streptopus amplexifolius	H		4	1.63	3				5	5
Streptopus lanceolatus var. *roseus*	H		3	1.15	3.7					4
Taraxacum officinale	H	€	5	0	9	1		9		9
Thalictrum pubescens	H		4	1.15	4					4
Thelypteris noveboracensis	H		4	2.5	3.8					X
Trientalis borealis	H		5	0.89	3.4	1		3		3
Trillium cernuum	H		5	1.41	3					3
Trillium erectum	H		4	1.91	4.5					4
Trillium undulatum	H		3	0	3					3
Urochloa xantholeuca	H		1		9					9
Viola adunca	H		1		7	1		6		7
Viola cucullata	H		1		3					3
Viola incognita	H		3	0	3					3
Viola macloskeyi ssp. *pallens*	H		4	1	3.5					3
Viola pubescens	H		3	1.15	3.7					4
Viola renifolia	H		4	1	3.5					3
Viola selkirkii	H		3	1.15	3.7					4
Waldsteinia fragarioides	H		3	1.53	6.7					7
Aulacomnium palustre	M		1		3	1		7	7	7
Barbilophozia barbata	M								8	8
Barbilophozia hatchery	M								6	6
Bazzania trilobata	M		3	1.15	2.3				5	3
Blepharostoma trichophyllum	M								5	5
Brachythecium populeum	M								4	4
Brachythecium reflexum	M								4	4
Brachythecium rutabulum	M									X
Brachythecium salebrosum	M		1		3				6	6
Brachythecium velutinum	M								5	5
Buellia disciformis	M		1		9				4	4
Callicladium haldanianum	M								6	6
Calypogeia neesiana	M								5	5
Campylium chrysophyllum	M								9	9
Campylium stellatum	M								8	8
Cladina rangiferina	M		2	0	9	1		3		X
Cladina stellaris	M		3	1.15	8.3					8
Cladonia cenotea	M								6	6
Cladonia coniocraea	M		1		3				5	5
Cladonia deformis	M								7	7
Cladonia mitis	M		3	1.15	8.3				9	9
Cladonia rangiferina	M		3	1.15	8.3				6	8
Cladonia squamosa	M								6	6
Cladonia uncialis	M		1		9				8	8
Climacium dendroides	M		2	1.41	2				7	7
Dicranum flagellare	M		1		3				6	6

Table 2 (*Continued*)

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Dicranum fuscescens	M		3	1.15	2.3				7	2
Dicranum majus	M					1		1	5	5
Dicranum montanum	M		2	0	3				6	3
Dicranum polysetum	M		2	2.83	5				6	6
Dicranum scoparium	M		2	1.41	2				5	5
Eurhynchium pulchellum	M		2	0.71	4.5				6	6
Graphis scripta	M								3	3
Herzogiella striatella	M								6	6
Heterocladium dimorphum	M								8	8
Hylocomium splendens	M		4	1.26	2.8	2	1.41	4	6	3
Hypnum lindbergii	M								8	8
Hypnum pallescens	M								5	5
Hypnum pratense	M								8	8
Hypogymnia physodes	M		1		1				7	7
Hypogymnia tubulosa	M								7	7
Jungermania leiantha	M		1		7				4	4
Lepidozia reptans	M								4	4
Leucobryum glaucum	M		1		3				5	5
Lobaria pulmonaria	M		2	4.24	6				5	5
Marchantia polymorpha	M		3	3.61	4	1		7	8	8
Mnium spinulosum	M								5	5
Neckera pennata	M								5	5
Oncophorus wahlenbergii	M								5	5
Paraleucobryum longifolium	M		1		3				4	4
Parmelia saxatilis	M								6	6
Parmelia sulcata	M								7	7
Parmeliopsis ambigua	M								6	6
Peltigera aphtosa	M		2	2.83	5					X
Peltigera canina	M		2	2.83	5				6	6
Peltigera horizontalis	M								5	5
Peltigera leucophlebia	M		1		6				5	5
Pertusaria amara	M								6	6
Plagiochila asplenioides	M					1		3	4	4
Plagiothecium denticulatum	M								5	5
Plagiothecium laetum	M		1		3				4	4
Platismatia glauca	M		1		3				7	7
Pleurozium schreberi	M		3	2.52	5.3	1		7	6	6
Pohlia nutans	M								5	5
Polytrichum commune	M		4	1.5	6.3				7	7
Polytrichum formosum	M					1		3	4	4
Polytrichum juniperinum	M		2	1.41	8	1		7	8	8
Polytrichum piliferum	M		2	0	9				9	9
Ptilidium ciliare	M		1		3				8	8
Ptilidium pulcherrimum	M								7	7
Ptilium crista-castrensis	M		3	1.15	2.3	1		3	4	4
Radula complanata	M								7	7
Ramalina fastigiata	M								7	7
Rhizomnium magnifolium	M		1		3				5	5
Rhytidiadelphus triquetrus	M		3	4.16	4.3	1		3	7	7
Sphagnum centrale	M		1		5				6	6
Sphagnum fuscum	M		2	1.41	8				9	9
Sphagnum girgensohnii	M		1		3	1		3	4	4
Sphagnum magellanicum	M		1		5				9	9

Table 2 (*Continued*)

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Sphagnum rubellum	M		1		7				9	9
Sphagnum russowii	M		1		5				6	6
Sphagnum squarrosum	M		1		3	1		5	5	5
Tetraphis pellucida	M								3	3
Thuidium delicatulum	M		2	1.41	2				7	7
Thuidium recognitum	M								5	5
Tortella tortuosa	M								5	5
Trichocolea tomentella	M		1		1				6	6
Ulota coarctata	M								6	6
Ulota crispa	M								4	4
Usnea filipendula	M		1		9					9
Usnea subfloridana	M		1		9				7	7
Abies balsamea	W		4	0	3	4	1.26	2.8		3
Acer pensylvanicum	W		2	1.41	4	2	0	1		3
Acer rubrum	W		4	1	5.5	6	1.67	5		5
Acer saccharum	W		4	1.15	4	4	0.5	1.3		4
Acer spicatum	W		5	1.48	5.2	4	1.26	3.3		5
Alnus incana ssp. *rugosa*	W		5	1.48	7.2	6	1.75	6.3		7
Alnus viridis ssp. *crispa*	W		5	1.67	7.6	2	2.12	6.5		8
Amelanchier alnifolia	W		2	1.41	8	2	0.71	7.5		8
Amelanchier arborea	W		3	2.52	5.3	1		1		X
Amelanchier bartramiana	W		3	1.53	6.7					7
Amelanchier laevis	W		3	2.52	5.3	2	0	1		X
Amelanchier sanguinea var. *gaspensis*	W		3	2.08	7.3	1		8		8
Amelanchier sanguinea var. *sanguinea*	W		2	2.12	6.5	2	3.54	5.5		X
Andromeda polifolia var. *glaucophylla*	W		4	1	8.5	1		9		9
Aronia melanocarpa	W		4	1	8.5	1		7		9
Betula alleghaniensis	W		5	1.48	5.2	5	1.64	3.8		5
Betula papyrifera	W		2	0	7	8	1.13	7.1		7
Cassandra calyculata	W		5	1.79	7.8					8
Chamaedaphne calyculata	W		3	1.15	8.3	2	1.41	8	7	7
Comptonia peregrina	W		5	1.67	7.4					7
Cornus alternifolia	W		5	1.67	3.6	1		1		4
Cornus canadensis	W		5	1.67	4.6	2	2.83	3		X
Cornus sericea ssp. *sericea*	W	$	5	1.67	6.6	1		9		7
Corylus cornuta	W		4	0.96	3.8	3	1.73	6		4
Diervilla lonicera	W		5	1.79	5.8	1		7		6
Fagus grandifolia	W		3	2.31	4.3	3	0.58	1.3		2
Fraxinus nigra	W		4	0	5	5	2.59	5.8		5
Ilex mucronata	W		5	1.79	5.8					5
Kalmia angustifolia	W		5	2	7	1		3	8	8
Kalmia polifolia	W		5	1.79	7.8					8
Larix laricina	W		4	0	9	6	0.52	8.7		9
Ledum groenlandicum	W		5	1.41	7	4	1.5	7.8		7
Lonicera canadensis	W		5	2	3					X
Myrica gale	W		5	0	9				8	8
Ostrya virginiana	W		2	2.83	5	5	1.34	2.4		X
Picea glauca	W		4	1.15	4	4	1.29	4.5		4
Picea mariana	W		4	2.31	5	5	1.82	4.6		X
Pinus banksiana	W		5	0.45	8.8	5	1.67	7.6		9
Pinus resinosa	W		4	1	8.5	5	1.22	7		8
Pinus strobus	W	$	4	1.15	6	6	1.03	5.3		6
Populus balsamifera	W		4	0	9	6	1.1	8		9

Table 2 (*Continued*)

Species	Str	Int	Experts			Literature			Ell.	I
			n	σ_e	$\bar{X}_e$	n	σ_p	$\bar{X}_p$		
Populus grandidentata	W		4	0	9	5	1.22	8		9
Populus tremuloides	W		3	0	9	8	0.83	8.1		9
Prunus pensylvanica	W		4	1	8.5	4	0.5	8.8		9
Prunus serotina	W	$	2	1.41	8	5	2	6		8
Prunus virginiana	W		5	2.41	3.6	2	0.71	7.5		X
Quercus rubra	W	$	5	1.1	6.8	4	1.29	5.5		7
Ribes glandulosum	W		5	1.79	3.8	1		5		4
Ribes hirtellum	W		4	1.91	3.5					4
Ribes lacustre	W		5	1.41	3	1		6		3
Ribes triste	W		4	2.52	3.5					3
Rosa acicularis	W		4	2.87	7.3					X
Salix bebbiana	W		4	1.15	8	4	0.82	8		8
Salix discolor	W		2	1.41	8	2	0.71	8.5		8
Salix eriocephala	W		1		9					9
Salix humilis	W		1		9	1		9		9
Sambucus racemosa ssp. *pubens*	W		4	1.71	4.8	2	1.41	6		5
Shepherdia canadensis	W		3	1.15	8.3	1		9		8
Sorbus americana	W		5	0.89	5.4	1		8		5
Sorbus decora	W		4	1.91	6.5	2	2.83	7		X
Taxus canadensis	W		5	0.89	1.6	1		3		2
Thuja occidentalis	W		5	1.67	3.4	4	2.16	4		3
Tsuga canadensis	W		3	2	3	4	0.96	1.8		3
Ulmus americana	W		3	2	7	4	1.71	5.3		6
Vaccinium angustifolium	W		5	1.79	6.8	1		3		7
Vaccinium myrtilloides	W		5	2.68	6.8					X
Vaccinium ovalifolium	W		3	2	3	2	0	1		3
Vaccinium oxycocos	W		4	2.83	7	1		9		X
Viburnum cassinoides	W		4	2.22	5.8					X
Viburnum edule	W		4	3.42	5.5	2	2.12	5.5		X
Viburnum opulus var. *americanum*	W		3	2	7					7

Strata (Column Str) refers to woody species (W = tree seedlings and shrubs), Herbaceous plants (H) and Bryophytes (M). Int column describe species native to Europe (€) and North American species introduced to Europe ($). n is the number of responses, σ the standard deviation and $\bar{X}$ is the mean. The Ell. column lists the Ellenberg index. The last column, I, lists our proposed synthetic index and X indicates species with broad amplitudes.

woody species: *Acer pensylvanicum*, *Amelanchier arborea*, *Amelanchier laevis*, *Fagus grandifolia*, *Kalmia angustifolia*, *Prunus virginiana*, *Ribes lacustre* and *Vaccinium angustifolium*. There was, however, little data for the genus *Amelanchier* which may explain its high variability. *A. pensylvanicum* and *P. virginiana* are non-commercial species and were not well documented in published data. The case of *F. grandifolia* is different because only one divergent response was given compared to five homogeneous ones. Thus, without this one ''outlier'' point, the result is very good. Furthermore, the value for *F. grandifolia* did match Ellenberg's index for *Fagus sylvatica*. The herbaceous species that were treated in the literature included *Calamagrostis Canadensis*, *Carex pensylvanica*, *Equisetum hyemale*, *Fragaria virginiana*, *Goodyera repens*, *Petasites frigidus* var. *palmatus*, *Prunella vulgaris* and *Sanguisorba canadensis*. There was a high variation in classification and this is probably due to lack of data and the fact that some families are not well-known (e.g. Poaceae). The same was true for the bryophytes and lichens (*Aulacomnium palustre*, *Cladina rangiferina* and *Marchantia polymorpha*).

Ellenberg et al. (1992) provides comparable data for three woody species, 50 herbaceous species and 86 bryophytes and lichens. The bryophyte layer alone contains 42 species for which we found no North American data, and four other species that have no

American counterpart. In most cases the value obtained for North America is lower than Ellenberg's index, but given that there are few data we feel that it is not appropriate to reject Ellenberg's value and thus we preferred to use the Ellenberg value as a final index. However, this should be taken into account when applying the index, and further testing of the given value and the North American result should be pursued. For woody and herbaceous species, there is a strong similarity between Ellenberg's index and the experts' responses reported here. It is similar for 64% of the species (difference < 1.50), and very similar for 26% (difference < 1.00), with only 9% of species that were very different. Some of the vascular species are native to Europe but were introduced to North America (Rousseau, 1968, 1974): *Achillea millefolium*, *Agrostis capillaris*, *Agrostis gigantean*, *Centaurea nigra*, *Galeopsis tetrahit*, *Hieracium caespitosum*, *Hypericum perforatum*, *Leucanthemum vulgare*, *Potentilla recta*, *Ranunculus acris*, *Ranunculus repens* and *Taraxacum officinale*. Only the results for *A. capillaris* and *R. acris* show a two point difference with Ellenberg, whereas the others species are similar to the European index. There are also North American species that were introduced in Europe: *Cornus sericea* ssp. *sericea*, *Epilobium ciliatum* ssp. *glandulosum*, *Pinus strobes*, *Prunus serotina* and *Quercus rubra*. Ellenberg has investigated *E. ciliatum* ssp. *glandulosum* and *P. serotina*, and his results are similar to those obtained here, with a difference of one point and two points, respectively. Surprisingly, Landolt (1977) gives a light level value of three in a nine level scale for *P. serotina*, that can be substantial since this species invades forest understories and supresses regeneration of other species (Starfinger, 1991, 1997; Starfinger et al., 2003). However, this behaviour may be simply a transitional stage. He also investigates *Q. rubra*, and his ranking was identical to ours and that of Gerhard Karrer (personal communication). However, *C. sericea* ssp. *sericea* seems to be very shade tolerant in Europe (Landolt, 1977). No European data were found for *P. strobus*.

Some species have a world-wide distributions and are consequently found in the Northern hemisphere as well as in the Southern hemisphere, such as *Cystopteris fragilis*, *Deschampsia flexuosa*, *Dryopteris carthusiana* and *Equisetum arvense* (Rousseau, 1974). For these species, expert responses and published data are similar to the European data. In the case of *D. flexuosa*, we used no published data, Rameau et al. (1989) who indicated a rank of mid-tolerant to intolerant, which is consistent with our ranking. Interestingly, all of these species are mid-tolerant and are found generally at the edge of forest paths. In the case of *D. flexuosa* Rameau et al. (1989) indicated a rank of mid-tolerant to intolerant and a wide range of different habitats such as forests of oak, beech, pine, alpine meadows or moors, which is consistent with our ranking. However, in Central Europe this species seems to be more shade tolerant and the corresponding Ellenberg's value is 6. As well as *D. flexuosa*, *D. carthusiana* has a wide range of habitats from pine forests and deciduous forests, to moors in Europe (Rameau et al., 1989). And as in Europe these species also covered a wide range of habitats in North America.

Other co-occuring species are either world-wide in distribution or they are circumboreal species, as is the case for most of the bryophytes and some of the vascular species (e.g. *Linnaea borealis*). It is possible that some are invasive species, but during the last 30 years the new intruders in North America originate mostly from Asia and have mostly become established along coasts and rivers, and not in forested areas (Claudi et al., 2002).

3.3. Examples of ranking

In many cases the general rule failed to give a consistent index, but we tried to capitalize on all of the available data. This task was done by studying each species case by case. As stated before for *Fagus grandifolia*, we obtained an answer outside of the range which drove the standard deviation away from our selection criteria. Raw results for experts were 3, 3 and 7, and for published data they were 1, 1 and 2. $\bar{X}$ are respectively 4.3 and 1.3 with σ equal to 2.3 and 0.6, and since these values do not match, the overall σ (2.23) is still too high. In this case we chose to eliminate the outlier, and an index of 2 was assigned. Concerning the choice between our results and Ellenberg's, two different cases appear. The first one is when our result is within two points of Ellenberg's, the second occurs when the difference is > 2. The first case can be illustrated by the results for *Equisetum hyemale*. The raw data were 7, 5, 4 and 9 for the expert opinion, which gives a mean response of 6.3. This can be contrasted with one published datum with a value of 3 and with Ellenberg's, value of 5. In this case, our result is near Ellenberg's but as mentioned earlier Ellenberg used a nine point scale level whereas we used a five point scale, which must then be expanded to nine for our results. Consequently, in cases of contrasts we favoured the more precise Ellenberg index. However, in the second case, our results are prefered and thus indicate a difference between the continents.

3.4. Robustness and adaptability

The procedure presented here has been applied to reduce or level out subjective interpersonal differences, but also to address smaller interspecific differences due to genetics or other geographical differences in ecological behaviour. The diversity of information that is integrated, experts' opinions as well as published data, make this index robust and widely applicable. This is the main difference with the Ellenberg approach (which is based primarily on experts' opinions and which has led to much criticism (Dierschke, 1994). The approach by indicator values has been extensively discussed (see Diekmann (2003) for a review), but despite criticism it is stated that ''the beauty of the system lies in its generality and robustness'' (Ewald, 2003). Moreover, it is possible to calibrate the values obtained for other parts of North America. Such a calibration has been made on Ellenberg's Central Europe indices for Britain (Hill et al., 1999, 2000), Sweden (Diekmann, 1995; Diekmann and Falkengren-Grerup, 1998), the Netherlands (Schaffers and Sykora, 2000) and Denmark (Lawesson and Mark, 2000). The methods they used have improved Ellenberg's values, and this is supported by the good correlation among all of these studies (Diekmann, 2003).

4. Conclusion

Our goal was to develop a shade tolerance index for understory plant species in northeastern North America as was done by Ellenberg et al. (1992) in Europe. An index was developed that will be consistent, robust and widely applicable. However, we acknowledge that the ecological preference of a species can vary within its geographical range. As stated before, the ''ecological existence'' was evaluated and not the ''ecological potential'' (Ellenberg, 1996; Whittaker et al., 1973) of each species, the former reflecting the ability of a species to generally persist at a given light level. If the light conditions change, the species may survive under stress for quite a long time. Consequently, this index should be used with caution when attempting to characterize light conditions using understory species as indicators.

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References

Anderson, R.C., Loucks, O.L., Swain, A.M., 1969. Herbaceous response to canopy cover, light intensity and through fall precipitation in coniferous forests. Ecology 50 (2), 255–263.

Baker, F.S., 1949. A revised tolerance table. J. For. 47, 179–181.

Bakuzis, E.V., Hansen, H.L., 1959. A provisional assessment of species synecological requirement in Minnesota forests. Univ. Minn., St. Paul, Minn., Minn. For. Notes No. 84, 2 p.

Beaudry, L., Coupé, R., Delong, C., Pojar, J., 1999. Plant Indicator Guide for Northern British Columbia: Boreal, Sub-Boreal and Subalpine Biogeoclimatic Zones (BWBS, SBS, SBPS and northern ESSF). British Columbia Ministry Forests Research, 139 p.

Brissot, M., 1972. Rachitisme ou coup de soleil? For. Privée Fr. 87, 27–34 (in French).

Burns, R.M., Honkala, B.H., 1990a. Silvics of North America. 1. Conifers, Agriculture Handbook 654, vol. 1. U.S. Department of Agriculture, Forest Service, Washington, DC, 650 p.

Burns, R.M., Honkala, B.H., 1990b. Silvics of North America. 2. Hardwoods, Agriculture Handbook 654, vol. 2. U.S. Department of Agriculture, Forest Service, Washington, DC, 877 p.

Claudi, R., Nantel, P., Muckle-Jeffs, E., 2002. Alien invaders in Canada's waters, wetlands, and forests. Nat. Resour. Can. 320.

Diekmann, M., 1995. Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. Ecography 18, 178–189.

Diekmann, M., Falkengren-Grerup, U., 1998. A new species index for forest vascular plants: development of functional indices based on mineralization rates of various forms of soil nitrogen. J. Ecol. 86, 269–283.

Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology: a review. Basic Appl. Ecol. 4, 493–506.

Dierschke, H., 1994. Pflanzensoziologie. Eugen Ulmer Verlag, Stuttgart, 683 p. (in German).

Ellenberg, H., 1979. Indicator values of vascular plants in Central Europe. Scripta Geobot. 9, 7–122.

Ellenberg, H., 1996. Vegetation Mitteleuropas mit den Alpen. 5. Aufl. Eugen Ulmer Verlag, Stuttgart, 1095 p. (in German).

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Zeigerwerte von planzen in mitteleuropa. Scripta Geobot. 18, 1–258 (in German).

Ewald, J., 2003. The sensitivity of Ellenberg indicator values to the completeness of vegetation relevés. Basic Appl. Ecol. 4, 507–513.

Gendron, F., Messier, C., Comeau, P.G., 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. Agric. For. Meteorol. 92, 55–70.

Grandtner, M., 1997. World Dictionary of Trees (available on-line the February 15, 2005 at http://www.wdt.qc.ca/).

Haussler, S., Coates, D., 1986. Autecological Characteristics of Selected Species that Compete with Conifers in British Columbia: Literature Review. FRDA Report, ISSN 0835-0752, 001.

Hess, G.R., King, T.J., 2002. Planning open spaces for wildlife. I. Selecting focal species using a Delphi survey approach. Landsc. Urban Plann. 58, 25–40.

Hill, M.O., Mountford, J.O., Roy, D.B., Bunce, R.G.H., 1999. Ellenberg's Indicator Values for British Plants. Institute of Terrestrial Ecology, Huntingdon, UK.

Hill, M.O., Roy, D.B., Mountford, J.O., Bunce, R.G.H., 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. J. Appl. Ecol. 37, 3–15.

Hutchison, B.A., Matt, D.R., 1977. The annual cycle of solar radiation in a deciduous forest. Agric. Meteorol. 18, 255–265.

Jobidon, R., 1995. Autécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec. Revue de la littérature. RNCanada Report No. 117, 179 p. (in French).

Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532.

Landolt, E., 1977. Oekologische Zeigerwerte zur Schweizer Flora, vol. 64. Veröff. Geobot. Inst. ETH Rübel, Zürich, 206 pp. (in German).

Lawesson, J.E., Mark, S., 2000. pH and Ellenberg reaction values for Danish forest plants. In: White, P.S., Mucina, L., Leps, J. (Eds.), Proceedings of the IAVS Symposium on Vegetation Science in Retrospect and Perspective, Uppsala, pp. 153–155.

Lin, J., Harcombe, P.A., Fulton, M.R., 2001. Characterizing shade tolerance by the relationship between mortality and growth in tree saplings in a southeastern Texas forest. Can. J. For. Res. 31, 345–349.

Messier, C., Doucet, R., Ruel, J-C., Kelly, C., Lechowicz, M.J., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29, 812–823.

Minnesota Department of Transportation, 2002. Plant Selector (available on-line the February 15, 2005 at http://plantselector.dot.state.mn.us/).

Rameau, J.-C., Mansion, D., Dumé, G., 1989. Flore Forestière Française: Plaines et Collines, vol. 1. Institut Pour Le Developpement Forestier, Paris, 1794 p. (in French).

Ritchie G.A., 1996. Trees of Knowledge: A Handbook of Maritime Trees. Canadian Forest Service Fo42-244/1996 (English edition).

Rousseau, C., 1968. Histoire, habitat et distribution de 220 plantes introduites au Québec. Nat. Can. 95, 49–169 (in French).

Rousseau C., 1974. Géographie floristique du Québec-Labrador. Distribution des Principales Espèces Vasculaires. Travaux et Documents du Centre D'études Nordiques 7, University Laval Press, 800 p. (in French).

Schaffers, A.P., Sykora, K.V., 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. J. Veg. Sci. 11, 225–244.

Shirley, H.L., 1943. Is tolerance the capacity to endure shade? J. For. 41, 339–345.

Starfinger, U., 1991. Population biology of an invading tree species—*Prunus serotina*. In: Seitz, A., Loeschke, V. (Eds.), Species Conservation: A Population-Biological Approach. Birkhäuser, Basel, Switzerland, pp. 171–184.

Starfinger, U., 1997. Introduction and naturalization of *Prunus serotina* in Central Europe. In: Brock, J.H., Wade, M., Pysek, P., Green, D. (Eds.), Plant Invasions: Studies from North America and Europe. Backhuys Publishers, Leiden, pp. 161–171.

Starfinger, U., Kowarik, I., Rode, M., Schepker, H., 2003. From desirable ornamental plant to pest to accepted addition to the flora? The perception of an alien tree species through the centuries. Biol. Invas. 5 (4), 323–335.

Whittaker, R.H., Levin, S.A., Root, R.B., 1973. Niche, habitat, and ecotype. Am. Nat. 107, 321–338.