Leaf area allocation as a guide to stocking control in multi-aged, mixed-conifer forests in southern Finland

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Summary

Two- and three-aged stands are alternative structures that can provide continuous cover and a diversity of tree sizes. The silviculture of these multi-aged structures consists, in part, of treatments to allocate growing space to understorey and overstorey stand components, and thereby affect stand increment and subsequent stand structure. A stocking assessment model was developed to assist with growing space allocation of pure and mixed-species stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) undergoing uneven-aged management based on data from a site in southern Finland. This model used individual tree leaf area, as represented by sapwood area, as a driving variable and stand leaf area index as a limiting condition. The model assists researchers and forest managers with the design and assessment of a variety of structures that might be formed by selection treatments. The model can estimate stem volume increment and average tree vigour under different stocking regimes. In comparison to observed results from a series of silvicultural treatment plots in southern Finland, the predictions from the model were good. The stocking assessment model is useful for assessing different allocations of growing space in stands with several age classes and stands undergoing conversion to uneven-aged management.

Introduction

Foresters in Scandinavian countries and in many other parts of Europe are under increasing pressure to develop alternative forest management systems to even-aged forestry. These pressures come from two primary sources: a general public dislike for the aesthetic qualities of even-aged systems (Holgen and Lind, 1994); and from the perception that uneven-aged stands provide greater environmental benefits – such as continuous cover and greater within-stand diversity –

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than even-aged stands (Hunter, 1990; Hansen *et al.*, 1991; Norokorpi *et al.*, 1994; Fries *et al.*, 1997). Variations of the systems used to maintain these uneven-aged structures may also be appropriate to transform even-aged stands to multi-strata, uneven-aged structures and to maintain these structures over time.

The most common procedures to allocate growing space among age or size classes in uneven-aged stands have used a diameter frequency distribution that is negative exponential or resembling a 'reverse-J' in form (Knuchel, 1953; Matthews, 1989; Schütz 1997; Smith *et al.*, 1997). These diameter distributions are generally assumed to represent equal allocation of growing space to all size classes and have therefore been described as 'balanced' (Smith *et al.*, 1997).

An alternative approach is to use some surrogate variable to represent growing space which can then be allocated to size or age classes. Long and Daniel (1990) presented a method to allocate stand density index – a relative density measure – among size classes. This method permitted unequal allocation of stand density index among size classes, but little justification for why one allocation might be superior to another.

Leaf area index (LAI) has been used as a surrogate for growing space occupancy in studies with even-aged stands because it reaches a maximum during stand development related to site quality and is highly correlated with stand volume increment (Waring, 1983; Long and Smith, 1984). O'Hara (1996) and O'Hara and Valappil (1999) used leaf area to represent growing space occupancy in multi-aged (stands with two or more age classes (Helms, 1998)) ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws) stands. Through the allocation of leaf area among age classes, O'Hara showed how a variety of multi-aged structures could be designed. Because of the strong relationship between tree growth and tree leaf area, tree and stand increment could be predicted given a particular allocation of leaf area. O'Hara (1996, 1998) advocated the design of multi-aged structures using a leaf area allocation approach and developed a model to develop guidelines for implementation of multi-aged management strategies for ponderosa pine.

Despite the apparent advantages of multi-aged (henceforth, multi-aged refers to both uneven-aged and two-aged stands) systems, little guidance is presently available to assist foresters with transformation of even- to multi-aged stands or the management of existing multi-aged stands. This paper attempts to address the following objectives:

1. Development of a stocking control model based on a leaf area allocation approach to guide management of multi-aged and multi-storied stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) on fertile sites in southern Finland. This model provides diagnostic information on average tree size, volume increment and tree vigour over a cutting cycle for multi-aged stands;
2. Validation of the model against stand-level data from the study site;
3. Develop applications for pure stands of Scots pine or Norway spruce, and mixed stands of these species;
4. Develop two example stands that are presented to illustrate possible applications of the model for designing multi-aged stand structures and for the transformation of even-aged to multi-aged structures.

Materials and methods

Study area

Equations used in the development of the stocking assessment model presented here were generated from data collected at the Vilppula Research Forest, in southern Finland (62°3'N, 24°15'E) (see O'Hara *et al.* (1999) for details). Treatments sampled included low thinning (four plots), single-tree selection (two plots), and untreated controls (two plots), plus three untreated plots in nearby stands. Species composition ranged from nearly pure Norway spruce (93 per cent of basal area) to almost pure Scots pine (99 per cent), but many had a significant component of broadleaved species (at most 43 per cent) such as silver birch (*Betula pendula* Roth.) and pubescent birch (*B. pubescens* Ehrh.). The selection plots and one control had a reverse-J-shaped (regularly all sized) (Lähde *et al.*, 1994a, b; Laiho *et al.*, 1995) stem distribution with spruce undergrowth. Plots treated with low thinning and one of the control plots had a normal, or bell-shaped, but fairly wide (over 20 cm) stem diameter distribution. All the plots were naturally regenerated and even-aged (age variation less than 20 years) (Laiho *et al.*, 1995), the age of dominant trees being about 40 years at breast height.

The three additional plots established in nearby stands of pure Scots pine had dominant ages of 17, 26, and 81 at breast height. The oldest stand had a younger age class of 16-year-old spruce. The other two plots were even-aged with some small spruce regeneration.

Sites were generally transitional between *Myrtillus* and *Oxalis–Myrtillus* site types (Cajander, 1949). Site index fluctuated between 27 and 33 m for Scots pine and from 28 to >33 m for Norway spruce (100 year base) (Gustavsen, 1980). Study areas are described in more detail by Lähde (1992) and O'Hara *et al.* (1999).

Both selection plots were predominantly spruce and ranged from 50 to 74 per cent of spruce LAI in the overstorey trees (O'Hara *et al.*, 1999). Control plots, which were also primarily spruce, ranged from 41 to 56 per cent spruce LAI in the overstorey trees. Only two plots had significant amounts of pine in both over- and understorey trees. These untreated plots had 78 to 87 per cent of pine LAI in overstorey trees.

Developing the stocking control model

Estimation of leaf area For the Vilppula study, LAI was estimated using allometric relationships between individual tree sapwood area and leaf area (Waring *et al.*, 1982). For this study, sapwood/leaf area equations for Scots pine were based on work in southern Finland (Mäkelä *et al.*, 1995) and Norway spruce used results from Germany (Oren *et al.*, 1986). For management applications, LAI could be estimated from remote sensing, site index, measurement of litterfall, or through measurement of light interception (Vose *et al.,* 1994; Waring and Running, 1998). Allocations of LAI to stand components can be based on percentage allocations and do not require measurement. However, on dissimilar sites, detailed measurements will be needed and new increment/leaf area relationships developed.

Describing stand structures The increment and vigour of stands undergoing uneven-aged treatments can be predicted with equations from O'Hara *et al.* (1999) (Table 1) if some stand structure parameters are provided. Stand structure characteristics are described with the number of canopy strata (one or two), the number of species, and the number of trees per strata for each species. Additionally, the proportion of the leaf area, or growing space, occupied by each species, strata, and by the stand as a whole, must also be estimated by the user. By limiting the total allocation of leaf area, the total stocking is limited below a maximum. The allocation of leaf area to different strata and species represents the design of the target stand structure. Leaf area or growing space occupancy of the Vilppula sample plots is shown in Table 2 by species, strata, and for the entire stand to provide guidance in growing space allocations (from O'Hara *et al.,* 1999).

Ranges of total growing space occupancy, as represented by LAI, should reflect management objectives. Higher levels of LAI will increase gross wood volume increment, but will be likely to reduce regeneration potential for a new age class. Lower LAI generally results in reduced stand increment, increased regeneration, and possibly greater structural diversity and stand health or vigour. For example, lower LAI levels in the tree component might permit greater development of a herbaceous understorey.

Table 1: Equations to predict tree volume increment from sapwood cross-sectional area at crown base by species and crown class group (from O'Hara *et al.*, 1999)

Species/crown class group	Equation	*n*	R^2	Sy|*x*
Scots pine/understorey	$I_v = 0.064 \times A_s$	30	0.94	0.41 dm^3
Scots pine/overstorey	$I_v = 0.105 \times A_s$	94	0.96	2.23 dm^3
Norway spruce/understorey	$I_v = 19.662\ (1 - \exp(-0.0066 \times A_s)^{((1-0.316)^{-1})}$	204	0.94	0.48 dm^3
Norway spruce/overstorey	$I_v = \exp\ (-2.908 + 1.099 \times \ln A_s)$	68	0.80	1.25 dm^3

I_v = volume increment in dm^3, A_s = sapwood cross-sectional area in cm^2.

Table 2: Stand volume, average annual volume increment over previous 5 years, and leaf area index (LAI) of sample plots by species and canopy strata (from O'Hara *et al.*, 1999) (LAI totals by species may not add to plot totals because of rounding)

Treatment	Plot	Stand volume (m^3 ha^{-1})	Volume increment (m^3 $ha^{-1}a^{-1}$)	Stand LAI (m^2 m^{-2})	LAI by species (m^2 m^{-2})			LAI by species/strata (m^2 m^{-2})			
								SP		NS	
					SP	NS	BL	OV	UN	OV	UN
Low thin	21	245	12.9	4.0	0.7	3.3	0	0.7	0	2.2	1.2
Low thin	19	235	12.8	3.7	0.6	3.2	0	0.6	0	2.3	0.9
Low thin	38	240	11.6	4.7	0.1	3.8	0.8	0.2	0	3.2	0.6
Low thin	6	234	12.7	5.7	0.1	4.8	0.8	0.1	0	3.8	1.0
Selection	36	254	11.9	5.5	0.1	5.3	0.1	0.1	0	3.9	1.4
Selection	5	271	13.5	7.1	0	4.7	2.4	0	0	2.3	2.4
Control	54	336	11.3	6.1	<0.1	5.8	0.2	<0.1	0	3.3	2.6
Control	34	329	14.4	7.3	0.3	5.3	1.8	0.3	0	2.1	3.1
Untreated	A	172	10.1	2.4	1.2	1.1	0.1	1.0	0.2	1.1	0
Untreated	B	190	17.1	2.6	2.5	0.1	<0.1	1.9	0.5	0.1	0
Untreated	C	518	8.9	2.0	0.9	1.1	<0.1	0.9	0	0.9	0.2

SP = Scots pine, NS = Norway spruce, BL = broadleaved species, OV = overstorey, UN = understorey.

Upper limits of stand density in even-aged stands are generally recommended to remain below about 60 per cent of maximum density (Drew and Flewelling, 1979; Long, 1985). These guidelines imply density dependent mortality is likely to occur at higher densities. Higher or lower levels of density may be used depending on management objectives, local site conditions, and species requirements. At Vilppula, where the maximum LAI for pure Scots pine and Norway spruce stands were ~2.5 and ~6.0 (O'Hara *et al.*, 1999), 60 per cent would be 1.5 and 3.6, respectively, for pure stands of these species. Mixed species stands of these two species can be weighted by the desired species composition to determine the maximum LAI. For stands with equal proportions of both species, maximum LAI would be 4.3 and the 60 per cent upper limit of a density management zone would be 2.6.

The Vilppula plots provide baseline conditions for assigning LAI to crown class groups in selection cutting treatments (Table 2). For example, LAI in a pure spruce stand might be evenly split between the upper and lower canopy strata. In mixed stands these allocations become more complicated. If LAI were allocated in equal amounts to the over- and understorey of both spruce and pine (each stand component), the likely result would be a severe suppression of the pine in the lower stratum. Because of its lower shade tolerance, Scots pine is unable to survive under a significant Norway spruce canopy. The allocations of LAI in designing uneven-aged structures for mixed-species stands must therefore also consider the relative shade tolerance of the component species since many combinations may not be possible.

The number of trees per species and crown class group are also a function of management objectives. For a given LAI, higher numbers of trees/ha will reduce average tree growth and result in smaller average tree sizes whereas lower numbers will have the opposite effect. Allocating a fixed amount of LAI over too many trees will also reduce average tree vigour and increase susceptibility to insects and pathogens.

Model calculations

Once the structure of the target stand has been designed, the increment of the stand can be estimated through a series of steps or individual calculations within a stocking assessment model. These steps can easily be organized in a spreadsheet to provide estimates of stand growth, and also allow a user to assess the merits of a given structure.

Dividing the LAI allocated to a species and crown class group (e.g. overstorey or understorey) by the number of trees gives average leaf area per tree for that crown class group. These average leaf areas were converted to sapwood cross-sectional area using relationships in O'Hara *et al.* (1999). These were then used in growth equations for each crown class group (Table 1) to estimate average increment per tree. Crown class group increment was the product of number of trees per component and average increment per tree. Stand increment is the sum of all component increments. To help with implementation of the structure, basal area for each crown class group can be predicted from average tree sapwood cross-sectional area (Table 3).

Model validation

To validate the stocking assessment model, volume increment for the study plots from Vilppula was predicted by using the LAI and number of trees by species (Scots pine and Norway spruce only) and crown class group for each plot in the model. LAI and increment from broadleaved trees was excluded because the model was developed only for Scots pine and Norway spruce. Each study plot was predicted as a separate model run. Model predictions were compared to observed volume increment reported in O'Hara *et al.* (1999) for only the conifer species.

Results

Model predictions compared with observed results

Model predictions for the Vilppula study plots compared quite favourably with the observed volume increment for Scots pine and Norway spruce (R^2 = 0.89; Figure 1A). No relationship was apparent between observed volume increment and LAI for Scots pine and Norway spruce (Figure 1B) or for all species combined (Figure 2 in O'Hara *et al.* (1999)). The inclusion of structural parameters that describe the location of leaf area and species in estimating increment as presented in the model (Figure 1A) were highly effective as compared to using only LAI (Figure 1B). These results also indicated the stocking assessment model approach was effective at estimating volume growth of stands with a diversity of structures.

Pure stand increment

Model results indicated stand increment increases with increasing percentage of total growing space occupied by overstorey trees for Scots pine (Figure 2). In these figures, all LAI, up to the maximum not occupied by the overstorey trees, was assumed to be occupied by the understorey. For example, if 80 per cent of LAI was occupied by the overstorey, then 20 per cent was occupied by understorey. However, LAI in these examples was constrained below a maximum of 60 per cent of maximum LAI or 1.5, or at 80 per cent of maximum LAI or 2.0 (Scots pine). In the Scots pine examples (Figure 2), an arbitrary density regime of 500 overstorey trees/ha and 1000 understorey trees/ha was used. Relationships were linear for Scots pine because the tree increment/leaf area (sapwood cross-sectional area) equations were linear (Table 1). Higher increment was achieved with higher total LAI.

For Norway spruce, two density regimes were tested: density regime A which consisted of 750 overstorey trees/ha, and 2000 understorey

Table 3: Equations to predict basal area of individual trees from sapwood cross-sectional area at crown base by species and crown class group

Species/crown class group	Equation	*n*	R^2	Sy|x
Scots pine/understorey	$A_b = 1.909 \times A_s$	30	0.92	14.8 cm^2
Scots pine/overstorey	$A_b = 3.202 \times A_s$	94	0.88	117.2 cm^2
Norway spruce/understorey	$A_b = 6.105 \times A_s^{0.6865}$	204	0.80	28.0 cm^2
Norway spruce/overstorey	$A_b = 2.067 \times A_s$	68	0.95	63.7 cm^2

A_b = basal area in cm^2, A_s = sapwood cross-sectional area in cm^2.

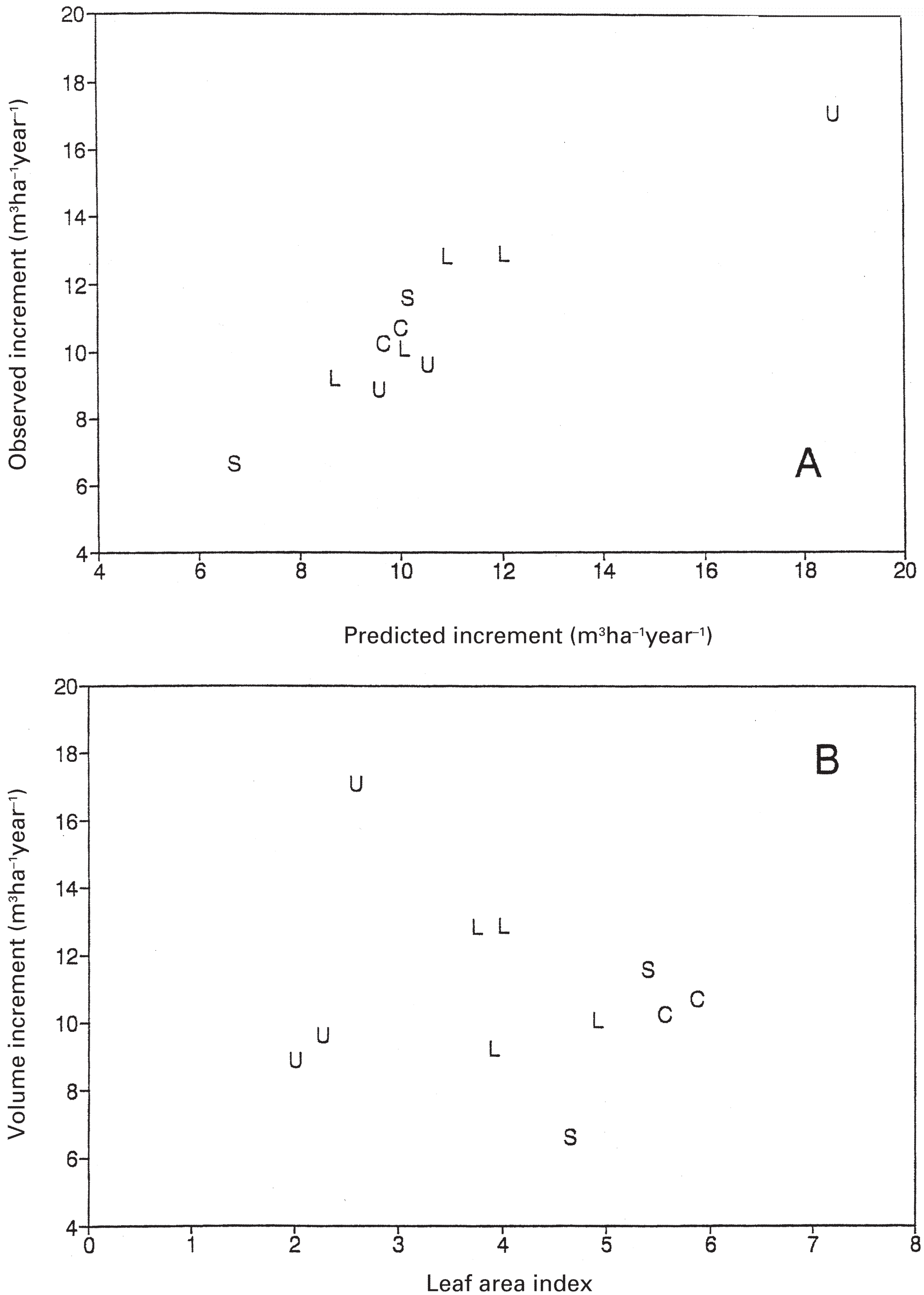

Figure 1. Observed and predicted increment for Scots pine and Norway spruce in Vilppula research plots (A). Increment and leaf area of broadleaved trees was excluded in making these comparisons. This relationship (observed increment = 1.73 + 0.66 × predicted increment; $Sy|x$ = 0.99 m^3 ha^{-1} per year) explained 88 per cent of variation in observed increment. In (B), no relationship was apparent between observed conifer volume increment and conifer LAI for the Vilppula research plots. Letters denote treatments: L = low thinning, S = selection cutting, C = Vessari control plots, and U = untreated Scots pine stands.

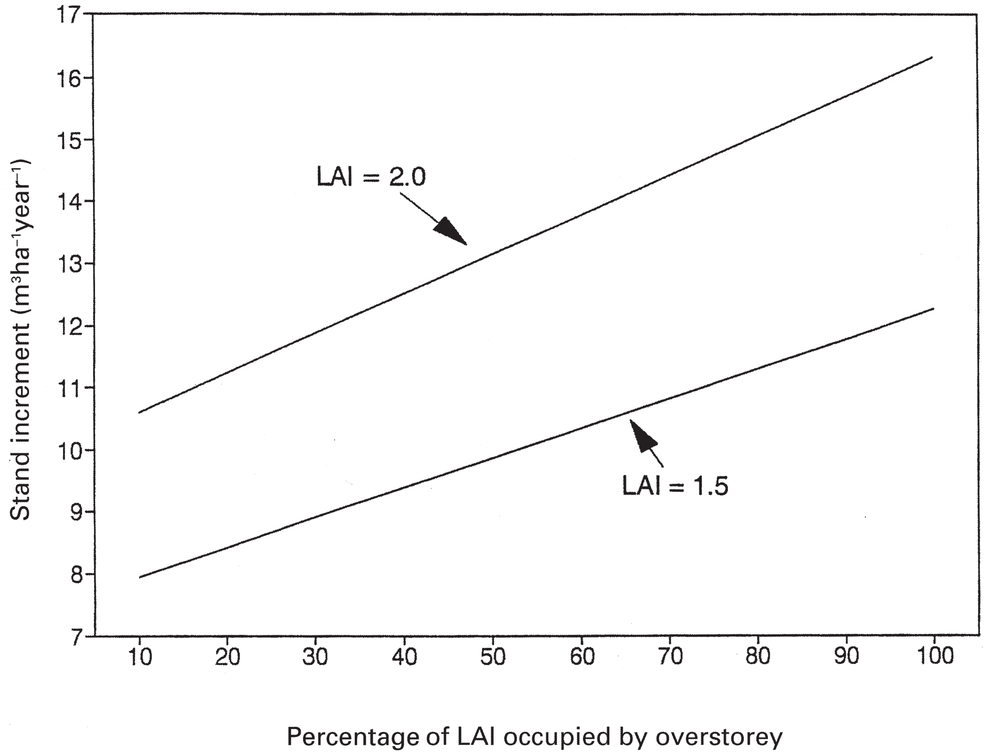

Figure 2. Volume increment over a range of overstorey levels of growing space (LAI) occupancy for Scots pine. Unoccupied growing space was assumed to be occupied by understorey. Two levels of LAI are compared.

trees/ha; and density regime B which included 500 overstorey and 6500 understorey trees (Figure 3). These were approximately the density regimes found in the two selection cutting treatments in the Vessari stand treatment study (O'Hara *et al.*, 1999). The two Norway spruce leaf area levels tested (3.6 and 4.8) coincided with 60 per cent and 80 per cent of the maximum of 6.0.

Volume increment increased with increasing percentage of LAI (growing space) occupied by the overstorey for Norway spruce (Figure 3). Relationships were nonlinear because of the nonlinear tree increment/leaf area (sapwood cross-sectional area) equations used in the model (Table 1). For a given LAI, density regime B had higher increment than density regime A when upper stratum LAI occupancy exceeded about 80 per cent. Apparently, when the allocation exceeded 80 per cent, the greater efficiency of the 500 overstorey trees in density regime B counteracted the low efficiency of having extremely high density in the understorey. At 100 per cent overstorey occupancy, the understorey was assumed to be nonexistent. At low allocations of LAI to the overstorey, neither crown class group in density regime B grew well.

Mixed-stand increment

Stands consisting of mixtures of Scots pine and Norway spruce exhibited similar growth patterns as pure stands. In these examples, both species were arbitrarily assigned 50 per cent of their upper limit LAI (pine 50 per cent of 1.5, spruce 50 per cent of 3.6) to give a total of 2.55. When one species was held constant at a 70 : 30 allocation of leaf area between over- and understorey, stand increment increased with increasing overstorey allocation of LAI of the other species

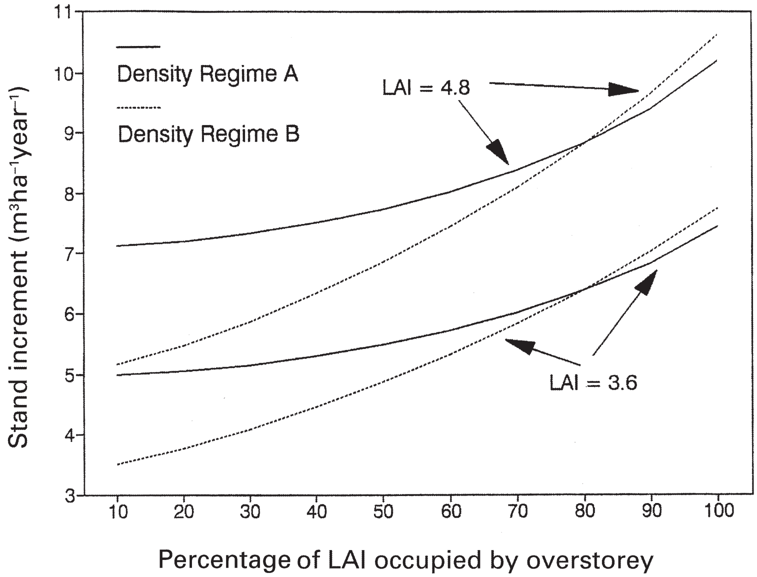

Figure 3. Volume increment over a range of overstorey levels of growing space (LAI) occupancy for Norway spruce. Two levels of LAI and two density regimes are compared. Density regime A = 750 trees/ha overstorey, 2000 trees/ha understorey stratum. Density regime B = 500 trees/ha overstorey, 6500 trees/ha understorey. At extremes of these simulated density regimes average sapwood area (crown size) may be larger in understorey than in overstorey.

(Figure 4). The relationship was linear for Scots pine and nonlinear for Norway spruce. Density regimes were held constant at 200 overstorey and 400 understorey trees/ha for both species.

More important than the total stand increment may be the individual tree growth rates. If, for example, overstorey trees were too crowded with low average leaf area (sapwood cross-sectional area), stand production may be adequate but individual tree vigour may be poor. If understorey trees were growing very slowly, their vigour may be insufficient to survive in an understorey environment, or they may not be capable of eventually replacing overstorey trees. Average growth rates of over- and understorey trees increased with increasing LAI allocation to that stratum for both species (Figures 5 and 6).

Estimations of stocking parameters

Individual tree basal areas within crown class groups were estimated from tree sapwood cross-sectional area. Equations for Scots pine overstorey and understorey crown class groups were linear (Table 3). The slope of the understorey equation was considerably lower than for the overstorey. This indicated an understorey tree will typically have a much lower ratio of basal area to sapwood area than an overstorey tree. For overstorey Norway spruce, a linear equation was used, while an exponential function provided the best fit for the understorey trees (Table 3). As with Scots pine, understorey trees had more sapwood per unit of basal area than overstorey trees.

Example applications

For applications on comparable sites, stand structures with two strata can be designed with the use of the stocking assessment model. Within ecological limitations of component species, allocations of number of trees and LAI per stratum and per species comprise the stand structure. For example, an even-aged, single-strata Scots pine stand might be converted to a two-aged, two strata stand by first thinning the overstorey to provide growing space to a new age class. Appropriate overstorey densities could be determined

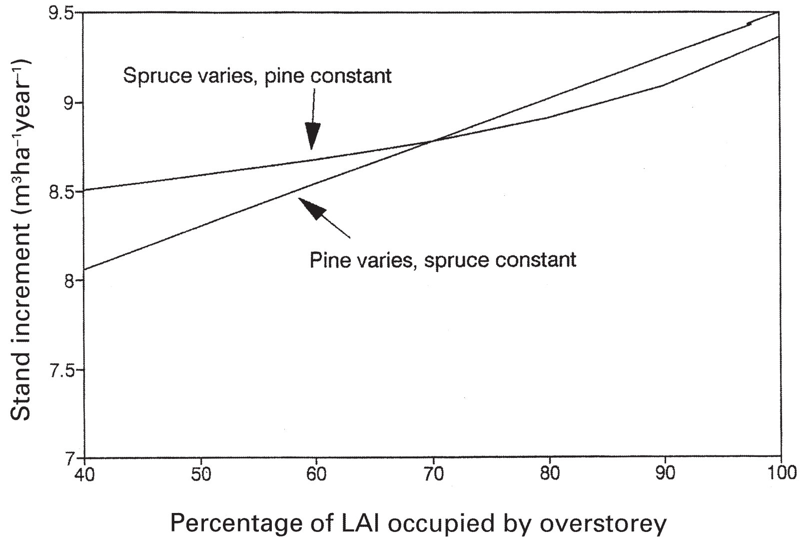

Figure 4. Volume increment for mixed stands of Scots pine and Norway spruce where spruce overstorey LAI varies for one relationship, and pine overstorey LAI varies for the other. A ratio of overstorey to understorey LAI of 70 : 30 was used for the species being held constant.

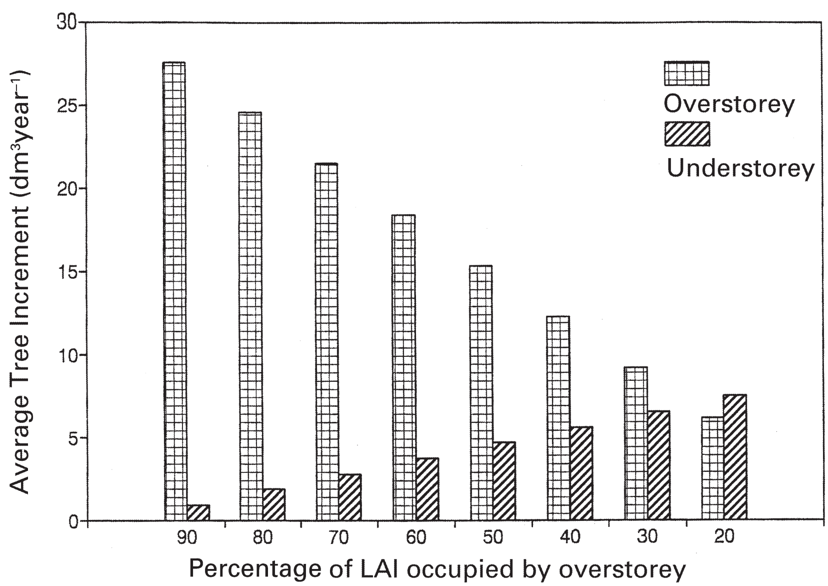

Figure 5. Volume increment for Scots pine over a range of overstorey levels of growing space (LAI) occupancy for mixed stands of Scots pine and Norway spruce. These results are for the simulations described in Figure 4 where Norway spruce growing space occupancy is held constant at 70 per cent overstorey occupancy and 30 per cent understorey occupancy.

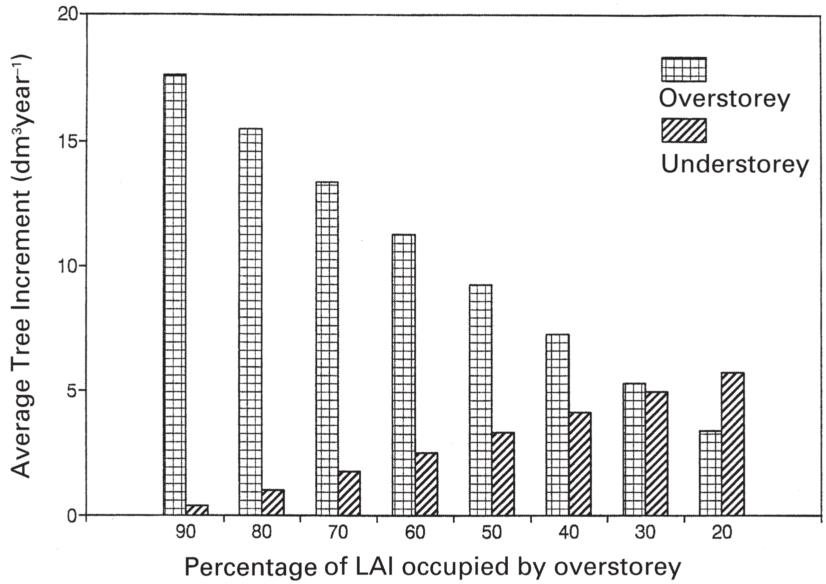

Figure 6. Volume increment for Norway spruce over a range of overstorey levels of growing space (LAI) occupancy for mixed stands of Scots pine and Norway spruce. These results are for the simulations described in Figure 4 where Scots pine growing space occupancy is held constant at 70 per cent overstorey occupancy and 30 per cent understorey occupancy.

by assessing their effect on understorey growth. The approach presented here could be used to generate a stand structure as in Table 4. In this example, reducing the density of an even-aged stand to 200 trees/ha and a LAI of 0.9 (70 per cent of a LAI of 1.25) should provide sufficient growing space for regeneration of a second age class. If the second age class is allocated 0.4 LAI for 250 trees, the resultant structure should grow 9.0 m^3 ha^{-1} per year during the subsequent cutting cycle.

If an existing two-strata structure with a predominance of Scots pine over Norway spruce was preferred, 80 per cent of LAI might be allocated to the pine and 20 per cent to spruce (Table 5). The allocations of growing space among the pine are 70 per cent for the overstorey strata, and 30 per cent for the understorey. For Norway spruce, allocations would be 25 and 75 per cent for the overstorey and understorey, respectively. The manager's intention would be to grow primarily Scots pine, but a significant percentage of Norway spruce is inevitable on this hypothetical site. There might be continuous Norway spruce regeneration, but most of these trees would be removed by thinning treatments before they reach the overstorey. The overstorey LAI for spruce is therefore kept low. The number of trees by crown class group would be 1000 and 1500 ha^{-1} for the over- and understorey for Scots pine, and 25 and 1000 ha^{-1} for the over- and understorey for Norway spruce. The total LAI, or growing space occupancy, would be 60 per cent of maximum levels or 1.5 for Scots pine and 3.6 for Norway spruce, and would be allocated with 80 per cent to Scots pine and 20 per cent of these amounts to Norway spruce.

With the equations presented in this paper, the stocking assessment model can be easily set-up in a spreadsheet. For this example, the model predicts a total stand increment of 9.5 m^3 ha^{-1} per year of which 91 per cent is from Scots pine (Table 5). Seventy-six per cent of this increment is from the overstorey. Mean tree growth rates range from 0.5 dm^3 per year for understorey spruce to 15.00 dm^3 per year for overstorey spruce. The model indicates this structure might be implemented by leaving 30.5 m^2 ha^{-1} basal

Table 4: Stocking example for conversion of a pure Scots pine stand to a two-strata, two-aged stand (the stocking allocations represent the target stand after a heavy thinning of the even-aged stand)

	Overstorey	Understorey
Percentage of growing space/species/crown class group	70	30
Number of trees/species/ha	200	250
Calculations for crown class groups		
Mean sapwood area/Tree (cm^2)	339.1	116.3
Mean tree increment ($dm^3\ a^{-1}$)	35.8	7.5
Mean tree growing space efficiency ($dm^{3\ cm-2}$)	0.11	0.06
Volume increment/species/crown class group ($m^3\ ha^{-1}\ a^{-1}$)	7.2	1.9
Basal area/species/crown class group ($m^2\ ha^{-1}$)	21.7	1.4
Stand-level totals (following treatment)		
Stand increment ($m^3\ ha^{-1}\ a^{-1}$)	9.0	
Stand basal area ($m^2\ ha^{-1}$)	23.1	

Stand structure parameters: total LAI = 1.25.

Table 5: Stocking example for mixed Scots pine/Norway spruce stand using the stocking assessment method (the total LAI would be 60 per cent of the maximum of 2.5 for Scots pine and 6.0 for Norway spruce; these LAIs were then split 80 per cent to Scots pine (LAI = 1.2) and 20 per cent to Norway spruce (LAI = 0.72))

	Scots pine		Norway spruce	
	Overstorey	Understorey	Overstorey	Understorey
Percentage of growing space/species/crown class group	70	30	25	75
Number of trees/species/ha	1000	1500	25	1000
Calculations for crown class groups				
Mean sapwood area/Tree (cm^2)	65.1	18.6	165.9	12.4
Mean tree increment ($dm^3\ a^{-1}$)	6.9	1.2	15.0	0.5
Mean tree growing space efficiency ($dm^{3\ cm-2}$)	0.11	0.06	0.09	0.04
Volume increment/species/crown class group ($m^3\ ha^{-1}\ a^{-1}$)	6.9	1.8	0.4	0.5
Basal area/species/crown class group ($m^2\ ha^{-1}$)	20.9	5.3	0.9	3.4
Stand-level totals (following treatment)				
Stand volume increment ($m^3\ ha^{-1}\ a^{-1}$)	9.5			
Stand basal area ($m^2\ ha^{-1}$)	30.5			

Stand structure parameters: Total LAI = 1.9, Scots pine LAI = 1.2, Norway spruce LAI = 0.7.

area. The model does not provide recommendations on selections of individual trees. These should follow conventional wisdom regarding leaving well-spaced trees of superior phenotypes.

Discussion

Model validation

A shortcoming of the validation procedure used in this analysis (Figure 1) is the model was tested on the same stands used to develop the model. However, this validation compared model results that were based on an individual tree, or stand structure approach, to a whole stand approach represented by LAI. Therefore, this is probably not a serious flaw to our approach. The improvement in the model over using LAI alone is substantial (Figure 1A compared with Figure 1B). This is a strong justification for the inclusion of stand structural parameters in models based on leaf area or other representations of space occupancy. Models which use average stand characteristics or stand-level totals to represent occupied growing space are treating all growing space as equal and are failing to consider the differences in productivity of different stand structure components.

Designing appropriate structures for multi-aged management

The methodology presented provides a means for assessing the volume increment, average tree increment, and subsequent development of stands managed with multi-aged structures. The relationships generated with the stocking assessment model are for a relatively small number of possible structures that could be designed for multi-aged management. Any number of other possible structures could also be designed and tested with the model. Although the magnitude of the relationships presented would vary with changes in the stocking parameters, the shape of these relationships is relatively constant because they are controlled by the shapes of the tree increment/leaf area (sapwood cross-sectional area) relationships (Table 1).

This preliminary stocking control procedure provides a means of regulating stocking using more of a first-principles approach to stocking control than previous stocking procedures that use basal area, trees per acre, or average tree size to represent growing space occupancy. At present, this procedure will be useful for researchers in quantifying the structures of different stand structures or to forest managers in designing structures to meet various management objectives.

The stocking control methods presented are significant departure from those used in the classical selection silviculture developed in central Europe. Rather than being primarily concerned with diameter frequency distributions, this approach attempts to use stand age classes, canopy strata, or species as a less arbitrary basis for division of growing space and designing stand structures (O'Hara, 1998). The greatest advantage of the stocking assessment approach presented in this study is its flexibility for designing stands with a diversity of structures without the limitations that have traditionally hindered selection silviculture. For example, constraining stands to diameter distributions defined with negative exponential distributions eliminates many possible uneven-sized or multi-aged structures that might follow other diameter distributions. These alternative structures represent important options for management that in many cases may emulate structures that develop following natural disturbance events. These procedures will be particularly effective in converting even- to two-aged stands as the initial step towards implementation of multi-aged systems and can serve as a basis for developing similar procedures for other forest types.

A disadvantage of the stocking assessment approach is the potential for users to design stands that are biologically unattainable. For example, the model permits the design of stands with high Norway spruce LAI in the overstorey and high Scots pine LAI in the understorey. Yet these structures could not occur because the shade intolerance of Scots pine would preclude it from growing in a heavily shaded environment below Norway spruce. LAIs are indicative of light interception, the light escaping through a full canopy of a shade tolerant species is insufficient for the growth and survival of a less tolerant species. The Vilppula study plot data (Table 2, from O'Hara *et al.*, 1999) can be used to guide the design of some structures.

Density management in mixed-species stands presents a more complicated challenge compared to single-species stands. For the stocking assessment model presented in this study, the species are separated and their LAI is used to estimate growth using unique equations. Many previous stocking control procedures have not distinguished between species and ignored proportional differences between stocking of mixed stands. Others have attempted to account for species differences through a variety of different means. For example, Hillebrand *et al.* (1992) used relative diameter and species to account for differences in relative density of mixed hardwood stands. In more complex mixtures, species may be assigned to groups or guilds of species that have similar ecological characteristics (Stout and Nyland, 1986). The approach used in this study accounted for differences in proportion of LAI for each species rather than tree density or basal area. Its effectiveness is demonstrated by the strength of the relationship in Figure 1A.

Uneven-sized vs multi-aged

At the time of measurement for this study, the selection treatments analysed at Vilppula represented the initial steps in the transformation of even-aged stands to a multi-aged condition. The description of these stands as uneven-sized (Lähde *et al.* 1994a, b; Laiho *et al.*, 1995) is appropriate in most cases given the existence of essentially a single age class over a broad range of diameters. Future treatments are likely to stimulate the development of new age classes as these treatments create canopy openings too large for existing trees to reoccupy. Once these age classes are initiated, these stands could also be referred to as multi-aged.

The age structure of these stands may influence the relations between tree increment and leaf area of understorey trees. O'Hara (1996) found younger age classes in multi-aged ponderosa pine produced less increment per unit of leaf area than older age classes. However, in these relatively open ponderosa pine stands, each age class generally occupied a unique canopy stratum and age was essentially a substitute measure for canopy position. An important question therefore concerns the importance of age in affecting the tree increment/leaf area relation. If tree age has no effect on the tree increment/leaf area relation, then the relationships developed on the even-aged, uneven-sized stands in this study will also be applicable to multi-aged stands. Otherwise new relationships should be developed.

The results from this study demonstrate that the growth and vigour of the understorey is dependent on the main stand (tree species, stem number, volume, and so on). After release and recovery, the understorey is likely to grow as fast as other trees of equal size regardless of age or whether it is Norway spruce (Cajander, 1934) or Scots pine (Vaartaja, 1951). Serious stunting, high age and large size do, however, hinder recovery (Vaartaja, 1951).

Further research needs

The procedures developed in this study are preliminary because of the narrow range of sites sampled, and the general homogeneity of the structures at Vessari. Additional research is needed which tests these results over a variety of sites to determine whether unique tree increment/leaf area relations would be found on sites with different productivity. It would also be useful to test the tree increment/leaf area relationships in stands having undergone a longer history of selection cutting than the 10 years at Vessari. Such stands would provide a greater range in understorey growth rates, leaf areas, and tree ages than were used to develop the stocking assessment model.

Research in other stands might also provide useful information on more creative distributions of stand LAI. For example, the higher productivity observed for uneven-sized stands in Finland (Lähde *et al.*, 1994a, b; Saksa *et al.*, 1995) may indicate these stand structures are a more efficient means of organizing leaf area than in even-sized stands. In this study, LAIs for selection stands (and untreated controls) were higher than the low thinned plots at Vessari (O'Hara *et al.*, 1999). These selection stands may be able to support higher LAIs through a more diverse distribution of LAI than comparable even-sized stands. Despite lower relative rates of increment of leaf area in the understorey, uneven-sized stands may compensate by supporting higher LAI and thus higher levels of stand increment. Further research is needed to examine the potential for uneven-sized stands to maintain higher LAI than even-sized stands over longer time periods.

Levels of growing space efficiency or growth efficiency for individual trees can be interpreted as measures of tree vigour (Waring, 1983; Münster-Swendsen, 1987). Some studies have related these measures of efficiency to tree mortality caused by forest insects (McCullough and Wagner, 1987; Amman *et al.*, 1988). Additional studies of these relationships for Scots pine and Norway spruce may provide some valuable insights into tree health that would be useful in designing uneven-aged cutting systems.

Foresters whose impetus for greater implementation of uneven-aged management is to enhance biodiversity will be concerned with maintaining a high level of tree species diversity. There will be considerable potential for mixed Scots pine/Norway spruce stands to revert to pure spruce stands with continued partial cutting unless adequate light levels are allowed to penetrate the overstorey. There is a need to study mixed-species stands that include Scots pine in the understorey to determine what overstorey LAIs are adequate for the development of this species.

Another priority would be development of local sapwood : leaf area ratios for Norway spruce. The ratios used by O'Hara *et al.* (1999) were from Norway spruce in Germany and may differ substantially from ratios in southern Finland. Whereas the use of sapwood cross-sectional area as the independent variable in individual tree analyses avoided any major problems, the sapwood : leaf area ratio from Germany (Oren *et al.*, 1986) was used to estimate stand-level LAI across the study plots (O'Hara *et al.*, 1999). Estimates of Norway spruce stand LAI are therefore suspect, as are the model-generated totals for LAI. The strong relationship between predicted and observed stand increment in this study reflects the consistency in the use of one sapwood : leaf area ratio for both segments of these studies. The potential for misinterpretation occurs if LAI determined with another ratio or other methodology is compared to the results from this study.

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