ANALYSIS OF COMPETITION IN SPRUCE-PINE-BIRCH COMMUNITIES IN CENTRAL SWEDEN

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Abstract

Visual estimates were obtained of the abundance of foliage for the different plant components in spruce, pine, and birch forests in central Sweden. The understory components were mainly dwarf shrubs, grasses, mosses and lichens. Sample sites for trees encompassed all edaphic conditions. Sample sites for the understory components encompassed the maximum observed range of vegetation composition for the dominant environment of each tree species. The results define the limits or possibilities to what occurs but not the probabilities of occurrence.

The composition of spruce-pine-birch communities by way of the occurrence and relative dominance of understory species/plant life forms was interpreted in relation to the dependence of a component on overstory vegetation and the relative nutrient requirements inferred from leaf longevities. It is suggested that the relative dominance of tree species reflects the interaction between water and nutrients in plant competition. The competitive situation for the understory components within birch and spruce systems is similar with grasses tending to exclude shrubs in the absence of trees. In pine systems the tendency was for coexistence of at least 3 components. Even with this floristically simple system the number of possible combinations made prediction of a successional sequence difficult, demonstrating that structurally complex systems can be obtained where few factors operate.

Introduction

Tunstall & Torssell (xxx) used the spatial variability in the relative proportions of the tree, shrub and grass components to interpret plant competition and succession in a eucalypt woodland. The approach combined traditional survey methods for native vegetation with plant competition theory derived from agriculture. They concluded that application of agronomic models to woodland systems was limited because the requirement for mutual exclusion was not met: a decline in one component of the natural vegetation did not necessarily result in its replacement by another. This situation is identified as deriving from the life cycles of plants.

Control of vegetation development by plant life cycles means that a significant proportion of the variation in community structure and composition reflects different temporal stages of development. Much of the spatial pattern in natural plant communities reflects different stages in a temporal development sequence. This time – space equivalence means that measurements taken at a single date in a heterogeneous system can potentially be used to describe long term successional patterns. This study applies the approach of analysing the heterogeneity of vegetation to Swedish forests to evaluate the extant factors generating variation in community structure and composition.

Swedish vegetation provides a marked contrast with complex Australian vegetation. Water is rarely limiting, the soils are recent in origin and represent varying degrees of sorting of mixed parent material (geologically simple), and all plants are subject to an extreme and extended winter period. The floristic composition is limited due to recent glaciation. In consequence the vegetation is dominated by only three tree species birch (*Betula alba*), pine (*Pinus sylvestrus*) and spruce {*Picea abies*). The broad ecology of the forests of central Sweden can largely be evaluated in terms of the competitive situations between birch, pine, and spruce and between each tree species and the understory components (mainly dwarf shrubs, grasses, mosses and lichens).

Methods

Measurements were obtained in the Kopparbergs lan of Central Sweden (60 N, 16 E) during May, 1978. Sampling was restricted to this region to avoid major climatic gradients. Spruce, pine, and birch were the dominant species and the few additional tree species were localised in specific environments. Lundgvist (1948) presents detailed geologic information and the general climatic and biogeographical considerations are given by Sjors (1965a, 1965b). The main geological categories are moraine (with variation in rock, boulders and fine particle size distribution), sedimentary sand (variable particle size distribution), organic soil-peat bogs, and fine sediments (clays). For comparisons between tree species all edaphic conditions were sampled. For comparisons between each tree species and the understory components sampling was restricted to deep sedimentary sand for pine, to moraine for spruce, and to rich moraine, fine sediments and organic soils for birch. These associations were selected as being the situation where each species competes most successfully.

Stands of vegetation were selected to encompass the full range of variation in vegetation (age, density, and composition). Vegetation recently (<20 yr) disturbed through commercial forestry practice was avoided. Within each stand the sample plots were selected to encompass the full range of variation in vegetation but with each plot chosen to be as uniform as possible. The minimum and maximum plot areas were 10 m^2 and 150 m^2 respectively. Smaller areas were used when characterising understory vegetation in monospecific tree stands and larger areas for evaluating trees.

The objective of the sampling procedure was to characterise all possible combinations of vegetation, not to obtain mean values for a particular stand or coop. While each sample necessarily relates to a finite area no effort was made to define the areal representation of a given sample. The data represent possibilities in identifying what can be observed to exist but not the probability of occurrence of any particular form of vegetation.

At each plot the projected foliage cover of each component was recorded as a measure of relative contribution. As foliage is the main functional unit of plants this provides a degree of equivalence between components having very different life forms. Projected foliage cover was used in preference to absolute leaf area because of measurement difficulties associated with the latter. In this study projected foliage cover appeared to provide a valid basis for comparison between the higher plant forms but lacked sensitivity with mosses and lichens. For these components the projected foliage cover was scaled relative to the depth of green foliage, the projected foliage cover being reduced in direct proportion to any decrease in foliage depth below the maximum recorded for that component.

All estimates were plot means and were obtained visually. The technique involved successive estimation of the abundance, and then the non-abundance, of a component in a plot until the estimates coincided. For trees this involved successive estimates of foliage cover and clear sky. Field tests on Australian vegetation identified that this method produced the same level and reliability of result for tree foliage cover as the use of crown ratios (Walker and Hopkins in

McDonald et al., 1984) and it has the advantage of not depending on the occurrence of circular crowns.

The characteristics recorded for each component were canopy cover (proportion of the plot area containing that component), foliage density (projected foliage cover within the defined canopy area), foliage depth (range of vertical distribution of foliage), and height (mean height of the uppermost foliage surface). The projected foliage cover is given by the product of the canopy cover and foliage density. Trees were aged by growth ring counts.

Results

Figure 1 presents the range of proportions of spruce, pine, and birch in a replacement diagram. As the sum of the contributions of the components varied greatly between plots all data in such plots have been normalised by presenting proportions. Although the assumption of mutual exclusion inherent in this diagram is not necessarily correct this figure demonstrates that every combination of the three species is possible. Excepting managed situations, pure stands of spruce, pine and birch are found mainly on moraine, deep sedimentary sand, and organic soils respectively.

The only absolute edaphic restriction was the absence of spruce on peat soils. The spruce-pine and spruce-birch combinations can therefore occur on all soil types except peat bogs but with the spruce-birch combination being rare on sedimentary sand. Natural birch-pine combinations are restricted to organic soils (peat bogs and high organic soils located between large boulders). In consequence no species is restricted by climate or, apart from spruce on peat soils, by substrate. The relevant feature of plant distribution therefore becomes the absence rather than presence of a species, and the dominance of a species in any location can be evaluated in terms of competitive interference.

In Fig. 1 the possible basis for plant competition is indicated. These suggestions are primarily based on relative leaf longevities, the ratio being approximately 1:4:8 for birch:pine:spruce. Considering leaf longevity as being a mean of nutrient conservation[1] this provides a ranking of the nutrient requirements of the species. A direct consequence of the leaf longevity with spruce is however the maintenance of a high leaf area with the approximate ratio for spruce to pine being 2:1. Considering that pine has a greater physiological control of water loss than spruce it is apparent that spruce has a much greater water requirement than pine.

The third factor indicated in Fig. 1, time, is manifest through the ability of spruce to regenerate under both pine and birch in situations where regeneration of these species is prevented. This is an empirical observation with an undefined physiological basis. It can only be suggested that the high leaf area of spruce provides advantage in competition for light and the nutrient conservation of advantage for survival under conditions of high competition for nutrients. This regeneration ability can therefore be regarded a consequence of the nutrient-water interaction.

These considerations suggest that the competitive situation between spruce, pine, and birch can be realistically evaluated in terms of a two factor interaction (Table 1) and such a concept has formed the basis for forestry classification of site potential in Sweden (xxx). However, a two factor interaction suggests that four tree species should exist. This appears not to occur because the low water situation is edaphically rather than climatically induced and the soil

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[1] Leaf longevity can be seen to reflect the balance between the energy cost of maintaining a leaf under unfavorable conditions and producing new leaf. It therefore reflects the balance between the duration and severity of the adverse conditions and the availability of nutrients.

factors generating low water availability are associated with low nutrient availability. The condition of high nutrients associated with low water availability effectively does not exist.

Table 1 Relationship between the occurrence of tree species and the combinations of high and low nutrient availabilities.

	Low Water Availability	**High Water Availability**
High Nutrients	na	Birch
Low Nutrients	Pine	Spruce

Replacement diagrams compare the relative proportions of the projected covers of the trees with two categories of the lower strata for spruce (Fig. 2a), pine (2b) and birch (2c). The others component is mainly composed of mosses and dwarf shrubs. With birch there is a tendency towards exclusion between grass and herbs with the dominance of a component depending largely on prior management. With the spruce system the grass and herbs tend to co-exist. Of the tree species only spruce can exclude all other components.

The results for spruce (Fig. 2a) and birch (2c) are similar in that grasses and shrubs do not co-exist without trees: there is a strong tendency towards exclusion. With birch a relatively high tree cover is required to maintain the presence of shrubs. These figures illustrate the general situation that in the absence of trees the grasses dominate but with trees present the tendency is towards a tree-shrub system and exclusion of grasses. The replacement diagram for pine (Fig. 2b) differs in that even though pure pine or shrub-moss systems were not found there are points in most areas of the triangle. Some areas of the triangle have few points and it appears that particular combinations might not be possible (eg. a lichen-tree system with a high tree proportion). However, examples of each two component mixture were found. This illustrates the main difference between the systems as with spruce and birch the tendency is towards exclusion while with pine the tendency is for coexistence of at least two other components.

Figures 3 and 4 compare the abundance of each dominant understory component with that of all taller components. For mosses (3b) and lichens (3c) this is the relative foliage cover of each component versus the sum of the projected foliage covers of all components excepting mosses and lichens. The data for mosses are for all systems but for lichens are from the pine system only as ground lichens are essentially excluded from spruce and birch communities. The high community cumulative projected foliage covers were obtained where *Vaccinium myrtillus* was a major component.

Simple relationships are not obtained as the data define areas rather than lines or clusters. The results identify the occurrence of a very large range in the total amount of vegetation in the systems and hence indicate a wide range of variation in resource utilization. As these data are from a wide range of edaphic conditions this reflects environmental as well as temporal variation. The results cannot be interpreted solely in relation to plant life cycles as was possible with those of Tunstall and Torssell (xxx).

Taking the data as defining the limit of the possible states, Fig. 3b illustrates simple competitive interference between mosses pines. This is similar to the relationship between grasses and trees in a eucalypt woodland (Tunstall & Torssell, xxx). However, the maximum level of moss occurred at an overstory projected foliage cover of 40% demonstrating a requirement for cover. At higher foliage covers competitive interference occurs with mosses as for all other species.

The relative height of shrubs in all systems was *Vaccinium vitis idaeus*, *Emperatum nigrum, Vaccinium myrtillus* and *Caluna vulgaris*. This sequence remained constant despite large variations in absolute height of these components. Problems in evaluating effective foliage height for grasses did not occur because of the exclusive condition between grasses and shrubs, so for each shrub species the overstory projected foliage cover could be readily determined.

In Fig. 4 the data for *V. myrtillus* are for all systems but hose for *V. vitis idaeus* and *Caluna* are restricted to pine. The results for *V. vitis idaeus* and *V. myrtillus* are similar to those for the moss with the greatest amount of shrub occurring where the overstory projected foliage cover was around 40%. With the exception of two points the only difference between the results in Figs. 3a and 3b is the magnitude of the response. For a given overstory the limit for *V. myrtillus* is approximately 1.5 times that of *V. vitis idaeus*. The two points that show high *V. myrtillus* at low overstory cover were from 60 and 70 year old spruce forests on fertile slopes where the density of the trees was low and had apparently been constant for most of the life of each stand.

Fig. 5 compares stand age with the projected foliage cover of pine. As with previous results the points define an area rather than a line so the results can only be used to define the limits of what may exist. The initial portion of the curve (< 60 yr) is well defined showing a rapid increase with time. The limit for old stands is not well defined because of the absence of data for stands older than 150 years but a general decline would be expected.

The data in Figs. 3 and 4 illustrate a dependency of the development of the lower strata on the upper strata and the data in Fig. 5 demonstrate that in even aged stands a wide range of tree cover can occur. While in young pine stands there will be a tendency for lichens and Caluna to dominate and in 60 year stands for V. vitis idaeus and/or V. myrtillus to dominate, persistent openings or gaps in stands will allow the Caluna and lichens to be present in stands of all ages. Thus for any particular stand there is no set successional sequence and within any stand a range of states can be observed. This does not mean that general changes in community composition will not occur as they can and do. It only indicates there will be a large variance associated with mean measures which will tend to mark the nature of the changes in vegetation.

An alternate approach to considering a linear successional sequence is to present a flow diagram of the possible changes in dominance of the understory components (Fig. 6a). The dashed lines represent progressions which are theoretically possible but were not observed in the short period of the observations.

The split between *C. vulgaris* and *V. vitis* idaeus is based on the level of cover, the progression from *V. vitis idaeus* (evergreen) to *V. myrtillus* (deciduous) on nutrients, and the progressions from both *V. vitis idaeus* and *V. myrtillus* to *C. vulgaris* and lichens on cover. The basis for the balance between *C. vulgaris* and lichens is not known. Mosses were not included as they tend to co-exist with the shrubs, particularly *V. vitis idaeus* and *V. myrtillus*.

The progression from *V vitis idaeus* to *V. myrtillus* could be based on time as the mean ages of the pine stands containing the four highest yields were 55 (43-90) for *V. vitis idaeus* and 90 (60-130) years for *V. myrtillus*. However, it is suggested that *V. vitis idaeus* coexists better with pine when competing for nutrients giving a resultant slower development for *V. myrtillus*. For spruce stands with higher nutrient availability than pine systems the maximum development of *V. myrtillus* occurred in younger stands and *V. vitis idaeus* was rarely dominant. Also, in one 43 year old pine stand exclusion of *V. myrtillus* by *V. vitis idaeus* was observed at a tree cover of 40% while *Vaccinium myrtillus* was dominant at tree covers around 20%. As the results indicate an equivalent response of these species to overstory cover this difference likely relates to competition for nutrients.

Figure 7a demonstrates a large number of possible successional sequences in a system with only four components. Taking the limits to the data in Fig. 5 however, some generalised sequences and be identified (Fig. 7b) but these need rarely be observed. This applies particularly in managed forests where thinning greatly modifies the patterns of change and often results in lichen dominated systems; the progression from lichens to lichens is much more rapid.

The time scales are approximate and indicate the period necessary for maximum development. Also, as these suggestions relate to the development of the pine population they do not contain considerations of the demographic characteristics of the understory components. To obtain a clear concept of the successional changes the demography for each component and its interaction with the others must be understood.

Discussion

The data describe the composition of forest communities in central Sweden. The description is based on structural attributes having functional significance and hence can be used to evaluate processes controlling the structure and composition of the vegetation.

The results illustrate a clear dependence of some species on overstory protection but the relationship between leaf longevity and nutrient requirement was based on interference in the absence of definitive data. The apparent anomaly between the suggestions that pine has a greater nutrient requirement and greater response to nutrients than spruce and the dominance of spruce on more fertile soils can be resolved by two considerations. Spruce appears to be excluded from the low nutrient soils through water and not nutrients and the higher nutrient response of spruce following a single fertiliser application is largely due to the duration of growth. The longer leaf longevity leads to a more persistent effect.

A feature of the nutrient relationships is the dominance of *V. myrtillus* in the shrub layer of spruce stands. As the suggestion was that *V. myrtillus* has a higher nutrient requirement than *V. vitis idaeus* the inference is that spruce has a poor ability to take up nutrients; that compared with *V. myrtillus* and probably pine it is a weak competitor for nutrients and so is dependant on efficient nutrient recycling for a reduced nutrient requirement. Species with this mechanism would be expected to show a large response to an increase in nutrient availability especially when compared to species relying on a high nutrient competitive ability. This suggestion of poor uptake ability also explains the absence of spruce on peat soils. While peat soils can contain large quantities of nutrients their uptake by plants is restricted by low pH and their being strongly bound to the organic matter.

A number of possible explanations exist for the positive relationship between a component and the level of overstory cover. With mosses a desiccation effect is possible and one suggestion is that this also occurs with *V. vitis idaeus* under conditions of high incoming radiation, no snow cover, and frozen ground. A second possibility is protection against radiation frosting. Without experimental data these hypotheses cannot be tested but an aspect of the distribution of *V. vitis idaeus* is that it occurs without overstory protection where the ground surface is highly irregular being associated with old tree stumps and with boulders. Because of this topographic effect only data for the pine system were presented for *V. vitis idaeus*.

The visual estimates provided sufficient accuracy to allow definition of the main characteristics of the systems. The use of successive approximation produces consistent estimates of cover but the comparisons were also aided by the form of analysis. The approach of characterising the variability rather than the mean increases the range of observations thus less accuracy is required for a given level of resolution than with conventional approaches. Also, the magnitude of the effects being examined is high. The maximum for the components were at 0 or 40% overstory projected foliage cover, the maximum projected foliage cover of *V. myrtillus* was 1.5 times that of *V. vitis idaeus*, while the leaf characteristics used were deciduous - non-deciduous and a longevity ratio of 1:4:8. However, the results in Figs. 2 and 3 involved summing up to four components hence the estimates were reliable and provided a degree of equivalence between components.

In this system the coexistence of higher plant forms requires markedly different physiological characteristics. A basis for this is given in the introduction, that the uniform severe climate and geologically uniform substrate greatly restrict the range of possible combinations of physiological characteristics resulting in differences being related simply to edaphic condition for trees and to edaphic condition and the development of the trees for the understory vegetation. However, even though the basis for the system composition is simple the large number of possible combinations results in an apparently complex vegetation.

The results define limits to what occurs but do not define the common or most likely occurrences. Within these limits there is a wide range of possibilities that could be regarded as reflecting stochastic variation deriving from the availability of recruits and/or edaphic variation. However, it is suggested that much is associated with the demography of the populations and hence life cycles of the plants.

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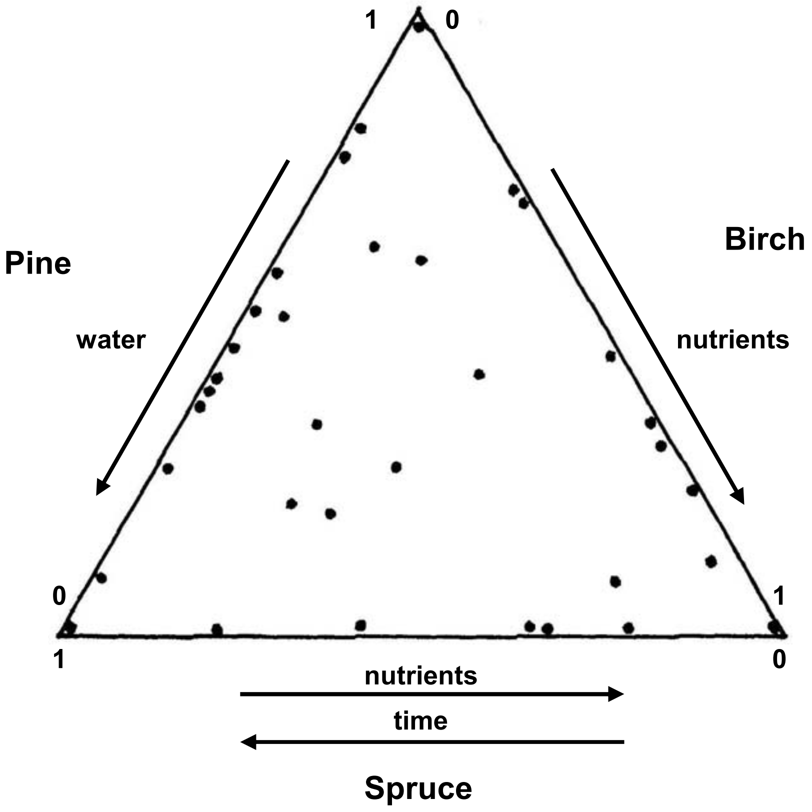

Fig. 1 Relative proportions of spruce, pine, and birch observed over all edaphic conditions.

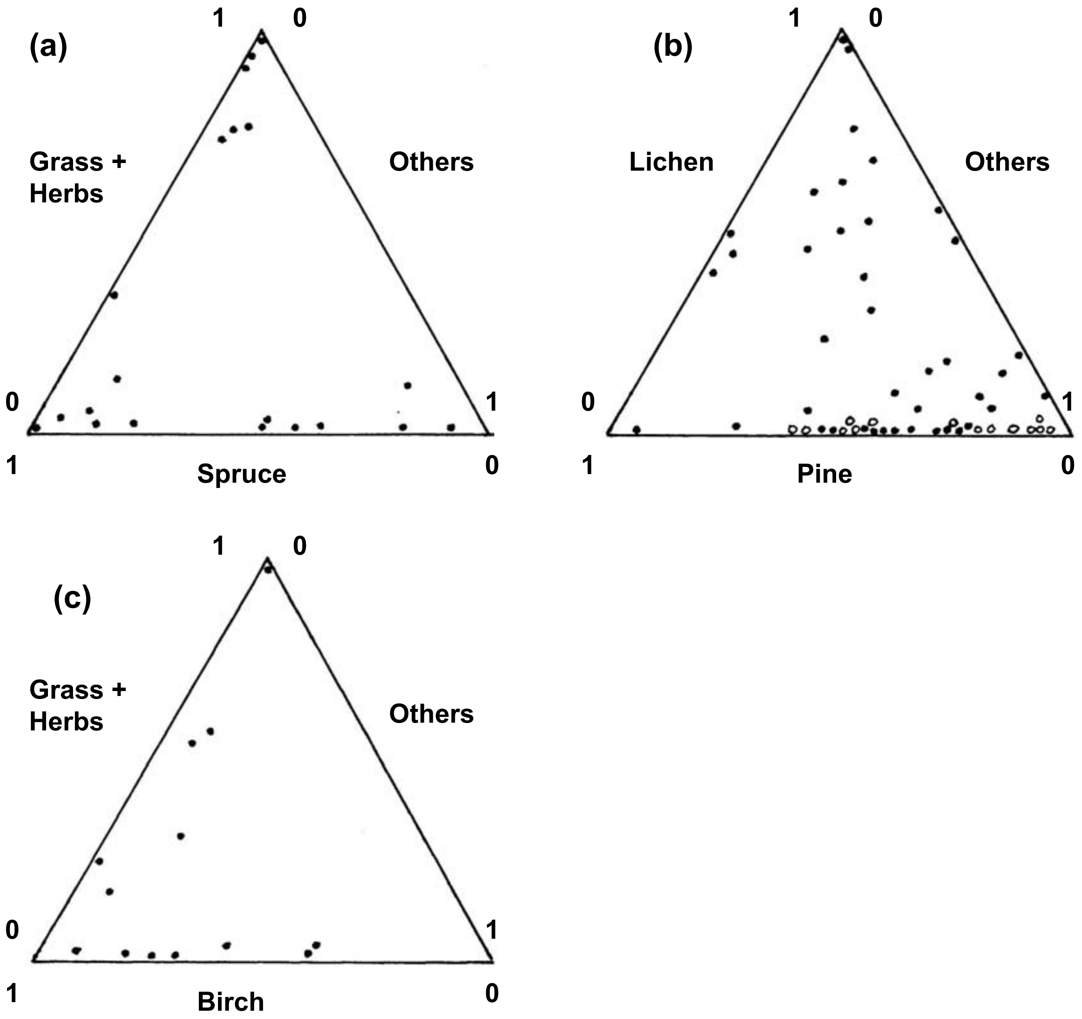

Fig. 2 Relationship between each tree species and the understory components. For all systems the understory component is composed primarily of dwarf shrubs and mosses.

(a) Spruce - grass + herbs - others
(b) Pine - lichens - others
(c) Birch - grass + herbs - others.

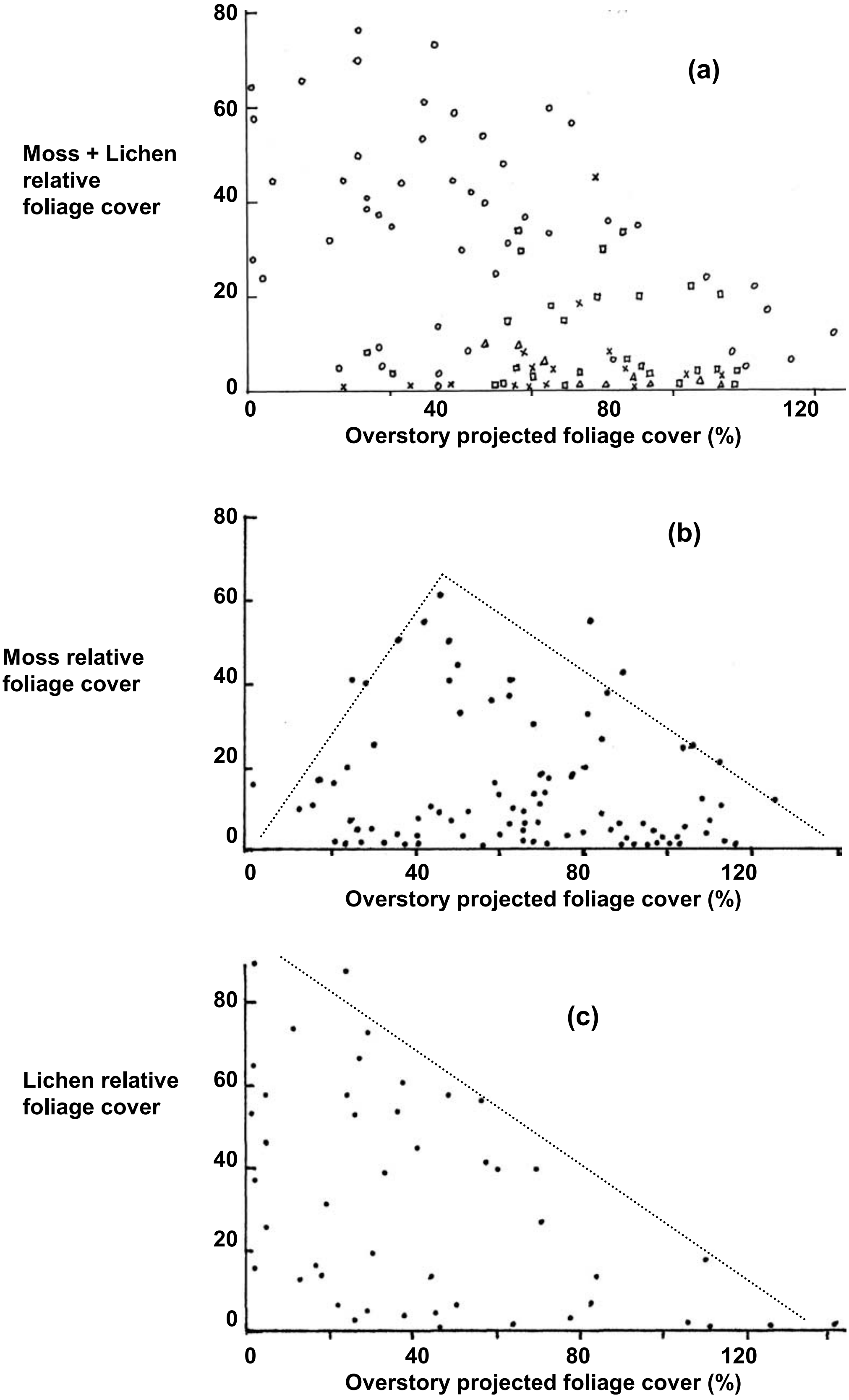

Fig. 3 The relationship between the relative foliage cover of mosses and lichens and the cumulative projected foliage cover of all other components.

(a) Mosses + lichens (all systems)
(b) Mosses (all systems)
(c) Lichens (pine systems)

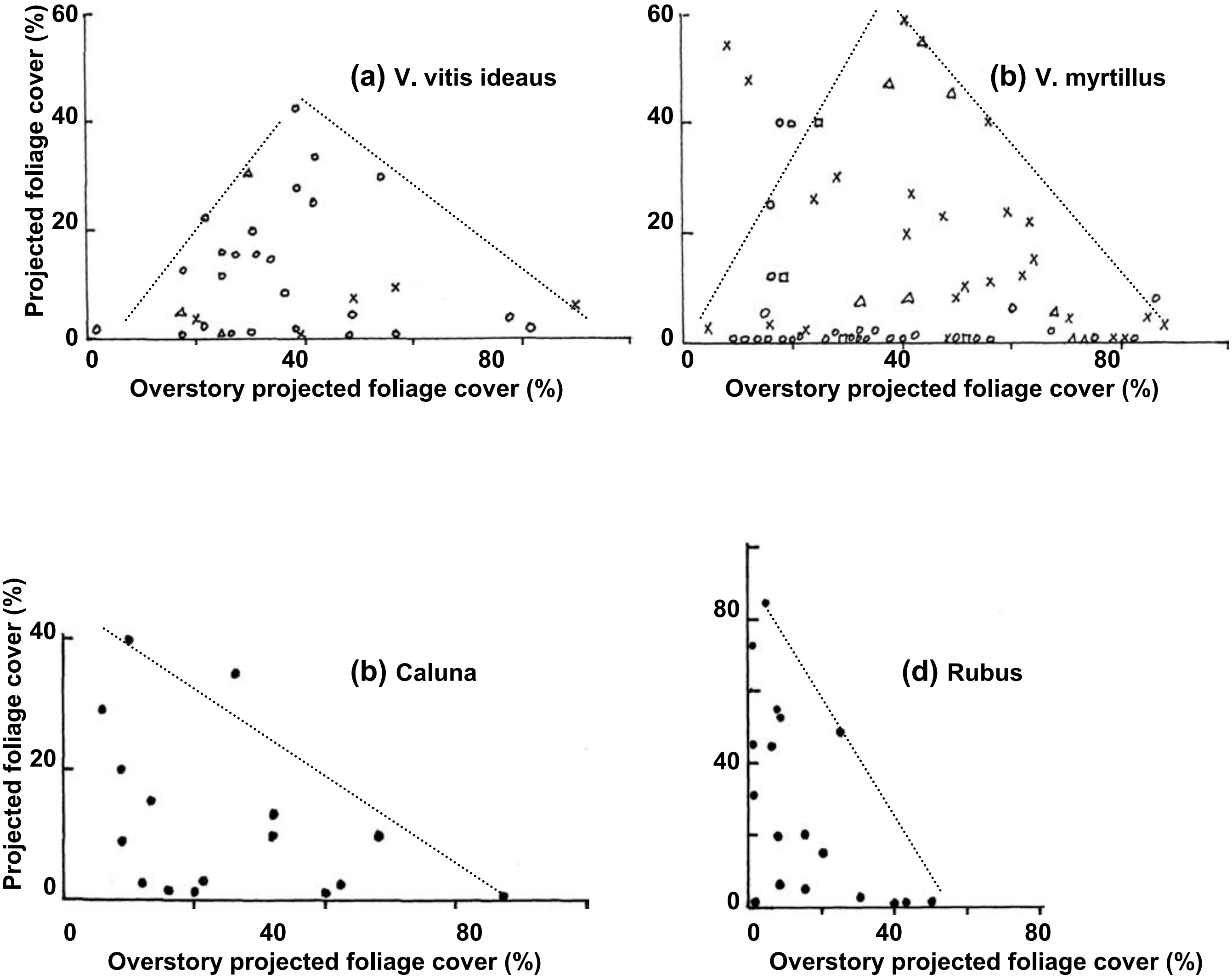

Fig. 4 The relationship between the projected foliage cover of each dwarf shrub and the cumulative projected foliage cover of all taller components.

(a) Vaccinium vitis idaeus (pine system)
(b) Vaccinium myrtillus (all systems)
(c) Caluna vulgaris (pine system)
(d) Rubus idaeus

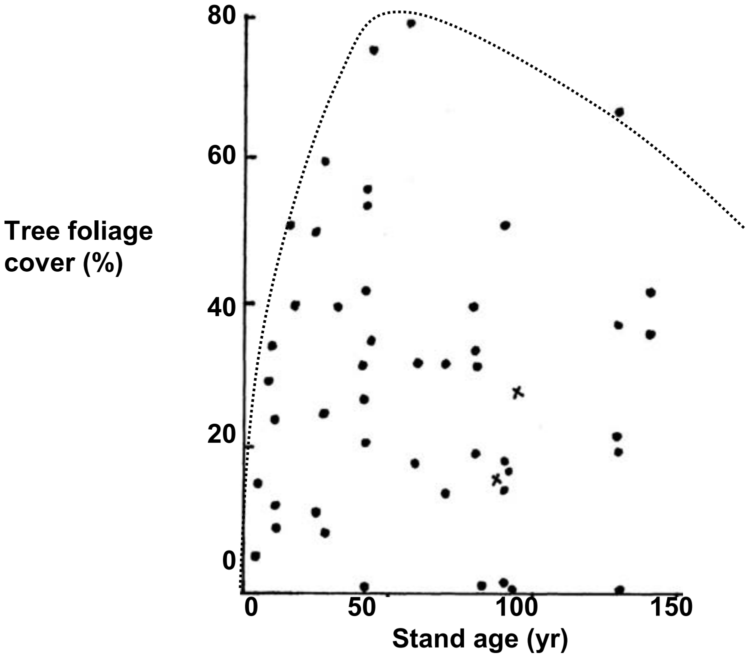

Fig. 5 Measured values of projected foliage cover for pine in relation to stand age.

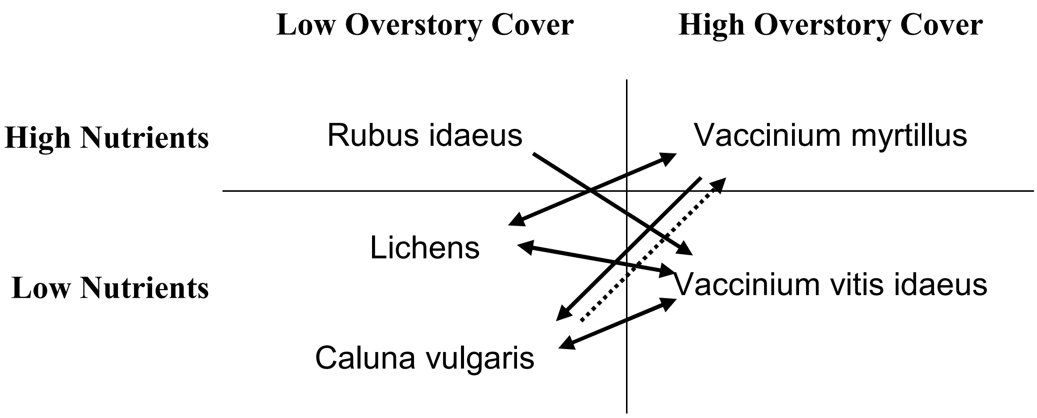

Fig. 6a Flow diagram of the possible changes in dominance of the understory components in the pine system.

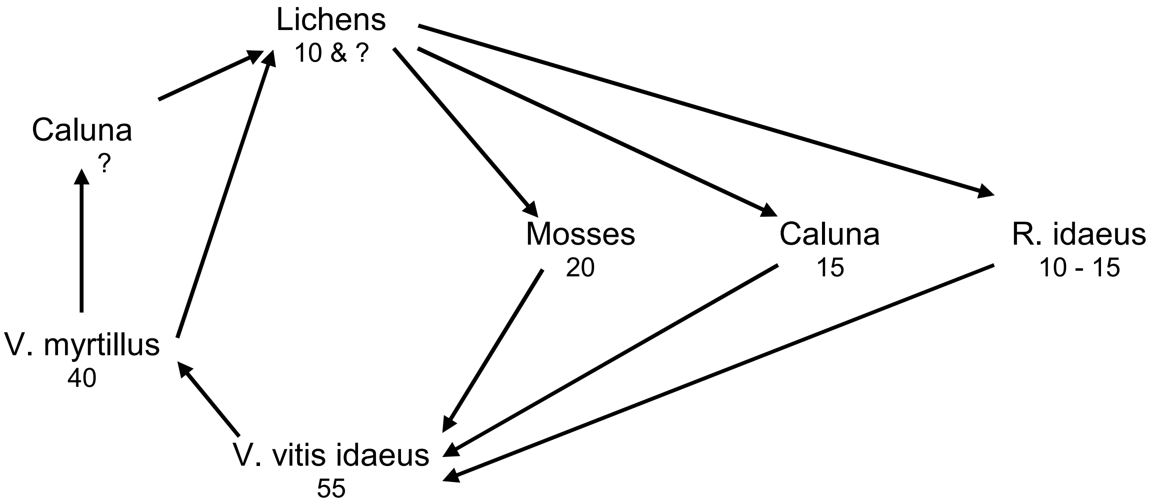

Fig. 6b Generalised successional sequence for the understory components of the pine system based on the nutrient and cover requirements of the components and the upper limit to the projected foliage cover - stand age relationship for pine (Fig. 5).