
The Influences of Neighbours on the Growth of Modular Organisms with an Example from Trees

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The influence of neighbours on the growth of modular organisms with an example from trees

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The growth and form of a modular organism is determined by the rigid rules of iteration (branching) and the differential response of each growing point to the local conditions around it. The degree of response of each individual module is itself dependent on the degree of physiological integration of the whole organism. Morphological continuity is a requisite but not a guarantee of physiological integration. In general, ‘phalanx’ growth-forms show more physiological integration than ‘guerrilla’ growth-forms. Trees, as an example of morphologically integrated modular organisms, show a variety of responses to the presence of modules both of the same and of different species. When two modules interact, three extreme responses are possible: (i) both modules stop growing or change their orientation, or both; (ii) one module is inhibited while the other continues its growth; (iii) neither is affected by the presence of the other.

The first case produces a clear separation (‘shyness’) between neighbouring modules both within and between trees. The second case produces a hierarchy of dominance-suppression. Finally, failure to ‘recognize’ the presence of a neighbour module may result in physical damage by abrasion of both participants. Under certain circumstances, this can also produce a visual impression of ‘shyness’. The importance of this ‘recognition’ mechanism is discussed for both modular animals and plants.

INTRODUCTION

Many modular organisms are sessile and grow by the iteration of some basic units of construction (modules *sensu* Harper 1981). In contrast to free-living organisms, sessile forms cannot usually escape the effects of competition by moving away from zones of high density of neighbours and establishing themselves in areas of lower density. The complex behavioural patterns exhibited by mobile animals are absent. One finds instead that both ‘search’ for resources and ‘escape’ from competitors occur through the adjustment of the morphological arrangement of modules. Two extremes of this morphological display are represented by the so-called ‘guerrilla’ and ‘phalanx’ growth forms (Lovett Doust 1981). Modules of ‘guerrilla’-type organisms are relatively widely scattered and separated from each other by long stolons, rhizomes or internodes; they are often produced by species that colonize and explore recently open habitats where neighbours are sparse. The ‘phalanx’-type form is more common in crowded environments; modules are densely packed and resist the invasion of space by modules of other organisms; they do not tend to explore but exploit the habitat already occupied.

Regardless of their position along this morphological continuum, as the population of modules grows bigger the effects of density are sensed in the immediate surroundings of the

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organism. The critical factor for sessile forms is the capture of space as a means of gaining access to more resources.

The response to local density has been studied in both sessile animals and plants. For marine animals, it has generally been assumed that competition occurs when there is limited physical space for attachment of organisms (Paine 1984). Buss (1980) has shown, however, that this competition for space can be mediated by competition for food. Neighbourhood models that predict the effect of local density on the performance of individuals have been developed for plants (Pacala & Silander 1985; Silander & Pacala 1985). From these studies it is clear that the performance of a modular organism is a function of the space that it captures through the multiplication of its constituent parts. An extension of this approach to account for space capture by individual modules belonging to the same and to different genetic individuals (genets) has been presented by Bülow-Olsen *et al.* (1984).

Since module display and resource capture are intimately related, one might expect individual modules to respond locally to the conditions in their immediate neighbourhood. Those modules that find themselves in favourable conditions should grow and multiply, while those in less propitious environments should produce copies of themselves at a lower rate or have increased risks of mortality. A modular organism with several axes of growth radiating into neighbourhoods containing different amounts of resources should grow at different speeds in different directions.

A growth programme that is responsive to local conditions and is not constrained by fixed, inflexible rules might seem the most efficient iterative method of growth. The adaptive or opportunistic reiteration of growth in angiosperms (Hallé *et al.* 1978) might then be interpreted as an improvement on the rather inflexible pattern of shoot module display of most gymnosperms. A programme that modifies the rules of growth with time has been called non-stationary by Waller & Steingraeber (1986) (and see Bell in this volume). If non-stationarity is expressed locally, as the conditions in different parts of the modular organism become more dissimilar, this is termed Markovian (Waller & Steingraeber 1986). This kind of growth programme implies a high degree of independence in the behaviour of each individual module.

The mechanisms by which modular organisms interact are still not well documented. A first step in understanding these mechanisms is the identification of resource depletion zones (RDZs) (Harper 1985). The RDZ of a module is the area of space around it where resources have been depleted to such an extent that there are insufficient resources to support the unimpeded growth of additional modules. In the simplest case, resource depletion is represented by situations in which one or a series of modules produce an umbra on modules positioned on the lee side with respect to the direction of resource movement. Examples of this kind are provided by upstream colonies of bryozoans that, by capturing food particles, deplete downstream colonies of essential resources (see, for example, Okamura 1984). The light depletion gradient in plant communities (Monsi & Saeki 1953) is an expression of this semicontinuous diminution of resources along a feeding hierarchy determined by the spatial position of modules. Within a physically interconnected modular organism (for example, a tree) there can be a strong hierarchy, determined not only by the spatial position of modules along the gradient of resources (height of the canopy) but also by the physiologically imposed hierarchy of (meristem) dominance (Maillette 1982*a, b*).

Degree of integration of modules

The degree of integration of a modular organism varies depending on the particular species and the conditions under which an individual develops (Winston 1978, 1979; Jackson 1979; McKinney 1984). Among colonial marine animals and pasture herbs the degree of integration is correlated with their growth form: guerrilla-type forms show less colony integration than phalanx-type forms (Jackson 1979; Schmid 1986). It is also correlated with the degree of specialization of individual modules: the presence of polymorphic zooids with specialized functions in bryozoans require a high degree of interdependence among members of the clone (McKinney 1984).

Even in highly integrated modular organisms, however, (such as siphonophores among animals, and trees among higher plants) the question of whether or not modules react individually to the conditions around them is far from settled. Morphological continuity between modules does not necessarily imply a high degree of physiological interdependence (see, for example, St Pierre & Wright 1972). In perennial forest herbs the degree of integration seems to be correlated with the risks of death of the individual ramet (Ashmun *et al.* 1982). Some experiments with grasses and other herbs indicate that physiological re-integration of physically connected parts can occur after defoliation or shading, at least for a brief period of time. The disturbed parts act in this case as sinks for assimilates (Ashmun *et al.* 1982).

The degree to which individual modules are independent or interdependent in their carbon economy has been reviewed for plants by Watson & Casper (1984). They concluded that, although there may be physical communication through very closed vascular systems, the movement of carbon between leaves is in general restricted by the vascular anatomy to those in neighbouring orthostichies. In experiments with grasses and sedges it has been observed that the flow of assimilates goes preferentially in the direction from parent to offspring meristems, although mature offspring can contribute reciprocally to parent (Marshall & Sagar 1968; Ong & Marshall 1979; Noble & Marshall 1983; Tietema 1980). The assumption that this flow determines the performance of daughter modules has been made in the modelling of branching in trees (Honda *et al.* 1981; Borchert & Honda 1984). Other simulation models do not include this assumption (see, for example, Aono & Kuni 1985) but can simulate branching structures that look like real trees (see also Bell, this symposium). These similarities do not, however, resolve the issue of whether the assumption of physiological interdependence of modules is necessary to mimic the morphology of the organism.

Growth and form in modular organisms

While growth may be defined as the change in the number of modules comprising an organism, form is a more elusive quantitative concept. To make comparisons on a continuous numerical scale, form can be defined as 'a relationship between real numbers' (Medawar 1945). If for example, we define form as the ratio between length (l) and width (w), a square will always be equal in form to another square, no matter how different in size they might be. However, a rectangle with $l > w$ will have a different form because this quotient will be greater than one. The reference point can be an external one and, for example, two rectangles with equal l and w , but the one lying horizontal and the other standing vertically, can be said to be different in form. The change in form from a rectangle with infinite width and finite length to a rectangle of finite width and infinite length is then a continuous function which can be used as a reference model in the study of forms on the plane.

This approach may be useful for unitary organisms but not in general for modular organisms. Since growth in the latter is potentially unlimited and branching (budding) can produce many different shapes, form cannot easily be defined. In modular organisms the most useful approach has been to identify the form of the individual module and then tackle questions on the nature of the self-similarity of the whole organism (for theories of self-similarity see Günther (1975); MacDonald (1983)). Two examples of this approach are the pipe-model theory of tree form (Shinozaki *et al.* 1964) and a similar approach to the study of growth form in fossil arborescent cheilostome bryozoans by Cheetham *et al.* (1981). These studies aim at the description of overall form as the result of a tightly controlled process that reproduces itself at all levels within the organism.

NEIGHBOUR EFFECTS ON THE GROWTH AND FORM OF MODULAR ORGANISMS

When modular organisms compete with each other the effect can be expressed as a change in the birth and death of individual modules (Bazzaz & Harper 1977; Whitney 1982; Franco 1985*a*; Hartnett & Bazzaz 1985; Jones 1985). The net result is a decrease in the growth rate of the population of modules. This, however, does not necessarily modify the self-similarity of the whole organism. So, for example, the linearity between the cross-sectional area of conducting tissues and the amount of leaves supplied, predicted by the pipe model, remains unaltered when trees are grown either isolated or in the presence of neighbours (Franco 1985*b*).

An approach to the analysis of growth and form of competing modular organisms

In this paper, I propose that a convenient way of summarizing the changes in growth and form of modular organisms, as determined by interference with neighbours, may be provided by focusing on the symmetry of the whole organism. The method used is the analysis of the distribution of modules around the central axis, the point of initial attachment to the substrate of the larvae or propagule, by using circular statistics (Mardia 1972; Batschelet 1981).

In the ideal situation, the polar coordinates of each module are recorded (figure 1). When modules are too numerous or when they are grouped on axes radiating horizontally from the central, vertical axis, the size (w , mass, diameter, length, etc.) of each secondary axis is measured and its orientation (θ) with respect to a reference point (north) is recorded. The rectangular coordinates of each secondary axis inserted in a reference circle of radius equal to one are calculated and weighted by their respective size. The rectangular coordinates of the mean angle are a weighted mean of the rectangular coordinates of each axis and are calculated according to the formulae:

$$x = \frac{\sum_i w_i \cos \theta_i}{\sum_i w_i}; \quad y = \frac{\sum_i w_i \sin \theta_i}{\sum_i w_i}.$$

The degree of asymmetry of the organism is estimated by the parameter r . This parameter is calculated as the Euclidian distance:

$$r = (x^2 + y^2)^{\frac{1}{2}}.$$

In physical terms, the parameter r represents the length of the standardized vector joining the geometrical centre of the unit circle with the centre of mass of the circular distribution of axes. When the circular distribution of the axes is perfectly uniform the value of r equals zero

(figure 1*a*). If these axes are bigger or tend to reorient themselves in a particular direction, the centre of mass will be eccentric to the geometric centre of the unit circle. This will be detected as an increase in the value of r (figure 1*b*). A value of r equal to one means that all the axes grow in the same direction (figure 1*c*). In practice, the value of the vector r will always lie between zero and one. The statistical significance of r as a measure of concentration depends on the sample size (number of modules or, for grouped data, number of axes of the organism). With the exception of figure 3, a value of r significantly different from zero ($p < 0.10$) is represented in this study by a continuous arrow of length r . A dotted arrow means that r is not significantly different from zero.

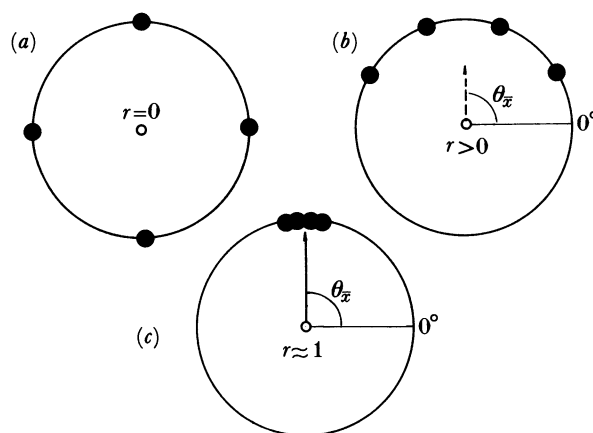


FIGURE 1. Mean angle ($\theta_{\bar{x}}$) and angular concentration (r) of three groups of four hypothetical points centred in a circle of radius 1.

The angular orientation of this vector (θ_x) can then be calculated (Batschelet 1981) as:

$$\begin{aligned} & \arctan(y/x) \quad \text{if } x > 0, \\ & 180^\circ + \arctan(y/x) \quad \text{if } x < 0, \\ & 90^\circ \quad \text{if } x = 0 \quad \text{and } y > 0, \\ & 270^\circ \quad \text{if } x = 0 \quad \text{and } y < 0, \\ & \text{undetermined} \quad \text{if } x = 0 \quad \text{and } y = 0, \end{aligned}$$

r is then an index of the degree of asymmetry of the organism and hence a measure of the relative intensity of competition on different sides of it. The method is similar to the vector analysis of Watson & Cook (1982) but is simpler and more amenable to statistical analysis and interpretation.

Neighbour effects on the symmetry of branching

The degree of asymmetry of competing modular organisms was investigated by using the annual plant, *Kochia scoparia* var. *culta* (Chenopodiaceae), as an experimental model of a tree, and three conifer species, *Picea sitchensis*, *Pinus contorta*, and *Larix kaempferi*.

Plants of *Kochia* were grown in a greenhouse in pots 23 cm in diameter and 18.0 cm in depth, filled with John Innes no. 2 compost. There were six pots and nine plants in the design. Three plants, approximately one-month-old, were each transplanted to the centre of separate pots. The other six plants were grown in pairs in three similar pots. These paired plants were placed

opposite to each other along the diameter of the pot and separated by a distance of 8 cm (4 cm from the centre of the pot). By growing single and paired plants it was intended to compare the asymmetry created by the presence of a neighbour with the radial symmetric growth of isolated plants. After transplanting, the plants were allowed to grow from 18 May to 7 August 1984. To prevent plants growing in the direction of a particular, unidirectional light source, the pots were periodically rotated. They were also periodically randomized on the bench in the glasshouse. On 7 August each branch was individually separated and weighed. Because the 2/5 phyllotaxis of *Kochia* determines rather precisely the position of each branch around the central stem, it was decided to divide the crown into eight equal sectors of 45° and the position of each branch was assigned to the sector containing its main bulk. The resulting data were grouped in eight mean angular directions. For grouped data the parameter r has to be corrected and for eight groups this correction factor is $\times 1.0262$ (Batschelet 1981). To relate the response in the reorientation of crown growth of paired plants a canonical correlation (Johnson & Wehrly 1977) was performed on the weighted sines and cosines of the angular orientation of the branches of each pair of plants.

In a second study, the growth response of neighbouring conifer trees was studied in Gwydyr Forest, North Wales. The intersection of three monospecific stands was chosen to investigate the response of individual branches to the presence of neighbour trees both of the same and of different species. The trees are located in the Ty'n-y-Mynydd block (national grid reference SH768594). They had been planted in 1959 and the plot was first thinned in the winter of 1983. The data were collected in the summer of 1983, before thinning. When the data were collected the canopy was closed and in places impenetrable. This suggested that interference between neighbour trees had taken place for several years.

To investigate the degree of branch asymmetry of these trees as a cumulative process throughout their life, the size variables used were the diameter and cross-sectional area, 10 cm from the insertion of the branch on the stem, and the total length of the network of each branch, that is the length of the main branch plus the length of second and higher order branches. Since leaves are produced uniformly along the branches in *Picea sitchensis* and *Pinus contorta*, network path length is directly proportional to the total number of leaves produced during the life of the branch (assuming no loss of dead shoots). For *Larix kaempferi* this is true for long shoots, but not necessarily for the short shoots. On the other hand, the cross-sectional area of a branch is assumed to be proportional to the amount of leaves present on it (that is, the prediction of the pipe-model theory (Shinozaki *et al.* 1964; Waring *et al.* 1982)). Since both branch diameter and network path length increase with the age of the branch, all three variables yield similar results. Therefore only the results using branch cross-sectional area are presented.

The orientation of each branch was measured by using a specially built protractor which could be opened and positioned around each tree. Attached to it was a compass which permitted the placing of the instrument in the same direction in all trees. Since both spruce and larch produce fairly linear stiff branches, only one measure of direction was necessary. In contrast, pine branches can become curved and reorient themselves. In this case, two measures of direction were recorded: (i) at the branch insertion; and (ii) at the branch tip, both with respect to the line formed by the centre of the tree and the magnetic north.

The position (height) of each branch along the stem and whether the branch as a whole was dead or alive were also recorded. For spruce and pine, branches were grouped in tiers. In the case of Japanese larch groups were formed every 50 cm along the stem.

The results are presented for (i) the whole tree; (ii) live and dead branches separated; (iii) individual tiers or groups of branches along the stem. In this last case it was not possible to perform a separate analysis for live and dead branches because the sample size was too small.

RESULTS

Kochia scoparia var. *culta*

Plants of *Kochia* growing singly in pots in the absence of neighbours develop a symmetric crown whose angular concentration (r) is not significantly different from zero (figure 2; table 1). Consequently, their mean angle of direction (with respect to an arbitrarily defined north (0°) at the beginning of the experiment) does not have any meaning. These isolated plants, however, seem to develop slightly more asymmetric crowns as their total size increases (table 1). This means that small differences in branch growth rate are accentuated with time.

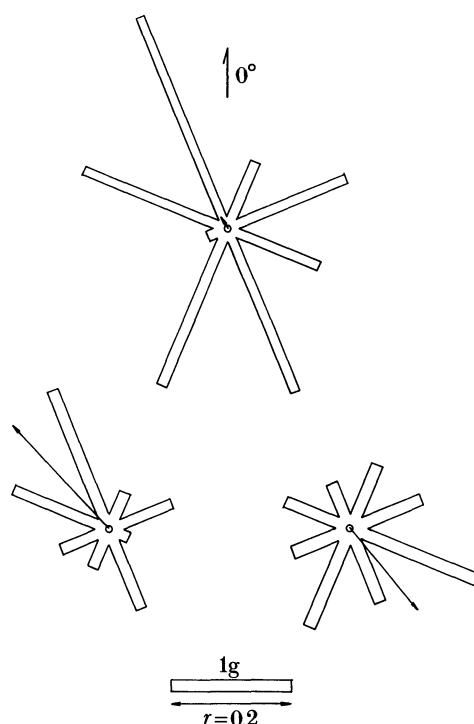


FIGURE 2. The symmetry of growth of the crown of one isolated and two competing plants of *Kochia scoparia* var. *culta*. The vector arrow projecting from the centre of the distribution of leaf mass in grams represents the mean angle; its length is equal to the angular concentration (r) of leaf mass in the crown. For scale, a vector equal to 0.2 and a bar equal to 1 g are shown.

When *Kochia* plants are grown in pairs they grow in opposite directions and away from each other (figure 2; table 1). This direction of growth is not necessarily on the expected $270\text{--}90^\circ$ plane formed by the centres of the two plants and seems to be related to the direction of their spiral phyllotaxis. The degree of asymmetry of these paired plants is accentuated by their total size, bigger pairs being on the whole more asymmetric (table 1). When one of the plants dominates over the other, the smaller plant has the higher degree of asymmetry (table 1).

TABLE 1. TOTAL LEAF MASS, ANGULAR CONCENTRATION (r), MEAN ANGLE ($\theta_{\bar{x}}$) AND DOMINANT CANONICAL CORRELATION (R_c) FOR CONTROL AND PAIRED PLANTS OF *KOCHIA SCOPARIA* VAR. *CULTA* GROWN IN A HEATED GLASSHOUSE AT PEN-Y-FFRIDD FIELD STATION, BANGOR, NORTH WALES, IN THE SUMMER OF 1984

control plants			paired plants			
leaf mass g	r	$\theta_{\bar{x}}$ deg	leaf mass g	r	$\theta_{\bar{x}}$ deg	R_c
8.786	0.019	325	4.615 2.893	0.048 0.094	351 143	0.836***
9.357	0.043	49	4.759 5.469	0.230 0.176	317 140	0.718***
12.892	0.141	20	4.935 6.969	0.156 0.115	354 211	0.914***

***, $p < 0.001$.

It is to be expected that neighbouring plants will grow into each other's resource depletion zones at a time determined by their size and their distance apart. Since these are continuous variables, the symmetry of branching may vary continuously from a uniform circular distribution when the plants are small or very isolated from each other, to a maximal asymmetry when the plants are large and close together. For this reason and to test the hypothesis that growth is reoriented towards the open side of the crowns, a canonical correlation between the weighted sines and cosines (Johnson & Wehrly 1977) of the branch angles for each pair of plants was performed. In all three cases, the canonical correlation was highly significant (table 1) indicating that individual plants do not integrate and average their growth in all directions but tend to grow in the direction where neighbours interfere least. This is despite the fact that the ordering of branches is only an approximation to the closeness of two 'equivalent' branches in the two plants.

Conifer species

Although the complexity of the interactions among several species in the natural environment might make an interpretation of dominance difficult, it proved possible to detect general patterns of crown response to neighbours in the three species studied. These responses are illustrated with three individual trees, one of each species.

Figure 3 shows the distribution of some of the trees studied at the intersection of three monospecific stands. The plot is close to an access road and the edge of the forest canopy is represented by the dotted line. To the left of this dotted line the forest spreads for more than 50 m. Only the trees in close proximity to those analysed in this study are shown. Their stems, with diameters drawn to scale, are represented by circles with letters standing for pine (P), spruce (S), and larch (L). The plot containing lodgepole pines is found to the upper left of the dashed line. The Sitka spruce stand is to its lower right. Japanese larch is restricted to the edge of the forest, along the road. The trees discussed in this and the next two figures have subscript 1.

Lodgepole pine seems to be the species that suffers most from the presence of either of the other two species. In particular, the individual at the centre of figure 3 shows clear signs of

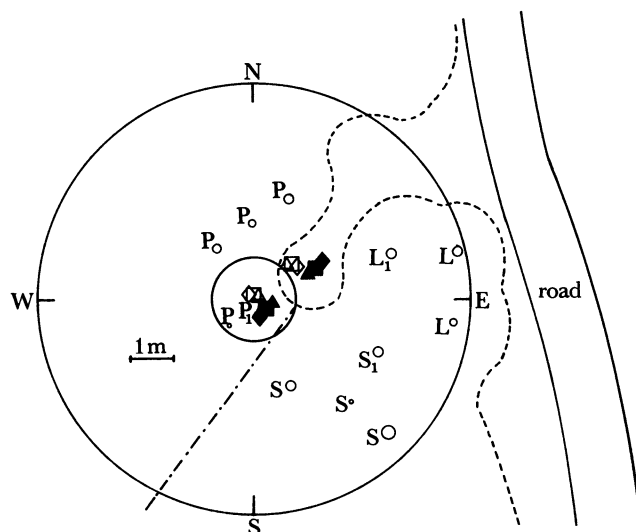


FIGURE 3. The growth response, as estimated by the angular concentration of branches (r), of a suppressed lodgepole pine (P_1) and the distribution of closest neighbour trees: (L) Japanese larch, (S) Sitka spruce, (P) lodgepole pine. The outer, bigger circle is an arbitrarily drawn circle, centred on P_1 , of radius 1. The inner circle has radius 0.2, which, given the amount of live (71) and dead (48) branches, is an approximate significance level ($0.05 < p < 0.10$) for values of r being greater than this value by chance. The triangles, squares, and diamonds represent the results of the circular analysis, that is, the values of r , inscribed within the unit circle. Their orientation with respect to the line formed by the centre of the circle and the magnetic north is the mean angle. The two groups of symbols inside the inner circle are the results for the angles of the branches measured at their insertion on the stem. The two groups outside the inner circle represent the results for the branch angles measured at the tips of the branches. (Δ , \blacktriangle) Live branches; (\diamond , \blacklozenge) dead branches; (\square , \blacksquare) total number of branches; (Δ , \diamond , \square) r calculated by disregarding cross-sectional areas of branches; (\blacktriangle , \blacklozenge , \blacksquare) r calculated by incorporating cross-sectional areas of branches.

suppression. This tree is surrounded by members of all the three species. Its stem diameter is only 7.1 cm compared with the diameters of the trees of the other two species which are on the average over 20 cm. All the individual pines around the experimental plot have diameters under 20 cm. Since the angular concentration of live and dead branches is almost identical, a look at the whole set of branches is sufficient to describe the direction of growth. Similarly, whether their sizes (branch cross-sectional area) are taken into account or not, the branches seem to grow and orient themselves in the same direction. The only difference in the results is between the orientation of the insertions of the branches and the orientation of their tips. For the former, no difference from a uniform circular distribution is detected (figure 3, symbols inside the inner, approximate significance level circle). This means that branches are produced in all directions. However, when the direction of the tips of the branches is used in the calculation of the rectangular coordinates of the mean angle, a significant direction of growth is observed (figure 3, symbols outside the inner circle). This direction of growth is so well established that it can be detected with or without weighting each individual branch by its cross-sectional area. As one would expect from a very shade-intolerant species, the branches of this tree have grown towards the only opening in the forest, the gap formed by the death of a (pine) tree 1.5 m northeast of it. This tree was the only one removed in this part of the forest and, counting the number of rings in the remaining stump, this removal occurred probably five years before this study was done.

Sitka spruce is the most shade-tolerant species of the three. This is reflected in the analysis

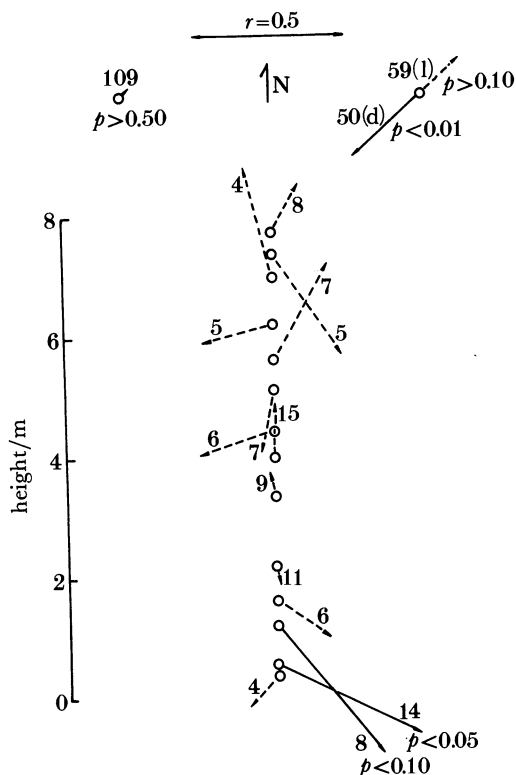


FIGURE 4. The response to neighbours of a dominant Sitka spruce (S_1 in figure 3). Mean angle (orientation of arrows with respect to the magnetic north) and angular concentration (r is the length of the arrows) of branches are shown for: (i) all the branches in the tree (upper left; $n = 109$); (ii) live ($n = 59$) and dead ($n = 50$) branches separated (upper right); (iii) each tier of branches along the stem (n shown for each tier). For visual aid in the interpretation, continuous lines are different from zero at a significance level of 0.10. For comparison a vector whose length is equal to 0.5 is also shown.

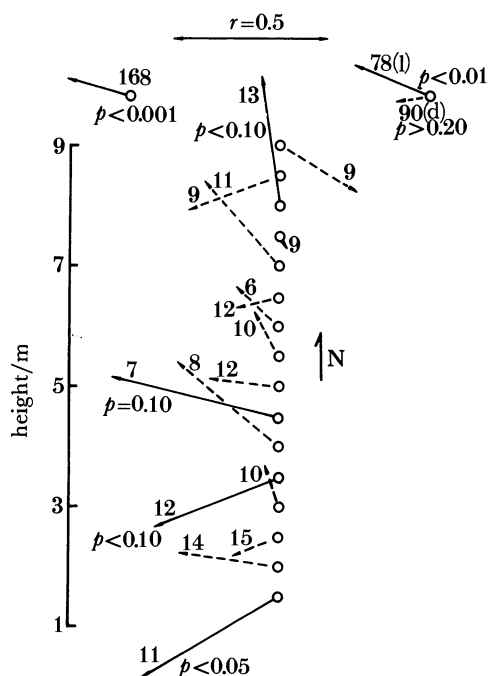


FIGURE 5. The response to neighbours of a codominant Japanese larch (L_1 in figure 3). Mean angle and angular concentration (r) of branches are shown for: (i) all the branches in the tree (upper left; $n = 168$); (ii) live ($n = 78$) and dead ($n = 90$) branches separated (upper right); (iii) each tier of branches along the stem (n shown for each tier). For visual aid in the interpretation, continuous lines are different from zero at a significance level of 0.10. For comparison a vector whose length is equal to 0.5 is also shown.

of the circular distribution of branches as a lack of preference in the direction of growth, except for the two tiers of branches near the bottom of the tree (figure 4). These lower branches, growing in the direction of the edge of the forest, have slowly gained access, throughout the years, to the east side of the plot where old branches of larch have started to die. None of the other tiers in the tree shows any particular, preferred direction of growth. When all the branches are considered together it is obvious that the tree grows and exerts its dominance in all directions (figure 4). It has a relatively thick trunk and branches profusely, being one of the dominant trees in this group. When live and dead branches are considered separately, however, dead branches seem to be grouped in the direction of the thickest part of the forest, that formed by the Sitka spruce canopy. Before the thinning of trees in the winter of 1983–4, this part of the forest was impenetrable, and only by breaking the old, dead branches could access be gained to climb and measure the trees.

The third example shows the results for a Japanese larch tree (figure 5). In this case the whole portion of the tree in close contact with neighbour trees (whole tree, live branches, and individual tiers) shows a preferential direction of growth towards the gap in the forest. Interestingly, this tree does not have a mean direction of growth pointing towards the north,

TABLE 2. (a) NUMBER OF LIVE AND DEAD SHORT SHOOTS ON NINE MIDDLE-CANOPY BRANCHES OF JAPANESE LARCH ORIENTED TOWARDS DIFFERENT NEIGHBOURHOODS

	open space	neighbourhood	
		larch	spruce
live shoots/dead shoots	289/146 (1.979)	66/92 (0.725)	324/98 (3.306)
	633/305 (2.075)	195/102 (1.912)	490/237 (2.068)
	1005/431 (2.332)	292/152 (1.921)	546/316 (1.728)

Notice how the ratio live to dead shoots (in parentheses) increases with the size of the branch for the open space and larch neighbourhoods but decreases in the spruce neighbourhood; shoot mortality increases by direct physical damage of long branches in the latter.

TABLE 2. (b) TEST OF INDEPENDENCE† OF THE THREE FACTORS INVOLVED: NEIGHBOURHOOD (*N*), BRANCH SIZE (*S*), AND SHOOT CONDITION (*C*)

interaction	degrees of freedom	residual deviance		
		live	dead	
<i>N</i> × <i>C</i> × <i>S</i>	4	57.69***		
<i>N</i> × <i>S</i>	4	live	21.42***	
		dead		
<i>C</i> × <i>S</i>	2	open space	30.73***	spruce
		2.76 n.s.		24.22***
<i>N</i> × <i>C</i>	2	small	0.37 n.s.	large
		61.58***		11.26**

n.s., Non-significant at $p = 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Figures are residual deviance of the maximal model and as such they represent a measure of interaction. The residual deviance is approximated by a χ^2 distribution with the degrees of freedom shown. One three-way model and eight two-way models were fitted. The latter were done on the corresponding two-way contingency tables for each factor level of the third factor.

† Log-linear model (Sokal & Rohlf 1981).

where interference is and has been presumably lower. The reason for this has to be looked for elsewhere: Japanese larch appears to continue its growth in the presence of the other two species but strongly reduces it in the presence of members of its own species (table 2). Branches of lodgepole pine stop or redirect their growth away from branches of Japanese larch and these in turn continue their growth. When branches of Sitka spruce and Japanese larch meet, physical damage by abrasion is produced causing the death of the leading shoots. New shoots arise from lateral buds and these in turn meet the same fate. The continuous production of new shoots in these 'stubborn' branches is accompanied by the laying down of new xylem. Consequently, their cross-sectional area also increases continuously. The tree has accumulated branch cross-sectional area in all directions except where new buds are not being produced, that is, where there are neighbours of the same species. One has to infer that this individual tree is not directing its growth towards the opening in the forest but that growth is severely inhibited by conspecific trees present on its east side.

DISCUSSION

It seems clear that trees are capable of responding locally to the interference imposed by neighbours both of the same and of different species. This response manifests itself both as a change in the birth and death rates of individual modules (Jones 1985) and an increased degree of asymmetry of the whole tree. The response seems however to be different depending on the neighbour species. The order of dominance observed in this study was Sitka spruce > Japanese larch > lodgepole pine. These results suggest that the artificial community formed by these three species in this plantation more closely resembles a hierarchy than a network of competitive interactions (for a definition of hierarchy and network kind of communities see Buss (1979) and Buss & Jackson (1979)). In theory, other factors being equal, Sitka spruce would eventually replace the other two species. It is known among foresters that the order of shade tolerance of these three species is spruce > larch > pine. This is reflected in the results.

It is tempting to make an analogy between the hierarchy observed and the continuum guerrilla–phalanx (Lovett Doust 1981). However, at least in conifers, the basic morphological patterns of module display are similar and differences are mainly expressed as different numbers of leaves or of short shoot modules and in frequency of branching by long shoots.

Looking at the interactions among the three species at a finer scale, the rank of dominance is not immediately obvious, at least for the dominant and intermediate species. This is because, in contrast to *Pinus contorta* which can change the orientation of its branches, the branches of *Larix kaempferi* and *Picea sitchensis* tend to grow straight and collide with each other before their bud birth rate is reduced and a reorientation of growth can take place (M. Franco & J. L. Harper, unpublished results). This means that Sitka spruce attains dominance after several years of enduring the constant clashing and death of meristems in the middle canopy, only because its higher rate of stem elongation permits it eventually to overtop the larch trees.

The branches of Sitka spruce are not very responsive to the presence either of members of its own or of different species. Although a reduction of growth occurs after several years of constant interference with neighbour trees, this reduction does not affect the degree of symmetry of the crown. This happens because by the time growth is diminished these branches are in parts of the crown that are heavily shaded anyway, if not by other trees, by the upper part of its own crown.

Japanese larch, with a relatively sparse crown, does not seem to be very responsive to the presence of the other two species. The shoots of Japanese larch are, however, very responsive to the presence of shoots of its own species. Although Sitka spruce produces a heavier shadow than Japanese larch, the elongation of axes of the latter is not suppressed by the presence of the former during the first years of growth, that is, in the upper parts of the canopy. Modules of these two species can then crash into each other causing physical damage by abrasion, with subsequent death of meristems. It is not until these meristems have died that the branch increases the frequency of long shoots on its lateral, secondary axes and spreads perpendicular to the direction of the neighbour tree.

Both Sitka spruce and Japanese larch retain dormant buds in the lower parts of their crowns but, since larch is less able to tolerate the shading imposed by both its own and neighbour's branches, they are less likely to produce long shoots and hence significant amounts of foliage later in life.

The differential response of branches growing in different neighbourhoods may provide some clues about the mechanisms that produce 'crown shyness' in trees (Ng 1980). This phenomenon occurs when a clear boundary gap is visible between the crowns of two trees, or between the branches of a single tree, producing a kind of loose jigsaw puzzle. The explanation advanced by Jacobs (1955) is that, by rubbing against each other in the wind, abrasion and death of branch tips is responsible for the spacing between crowns and branches (the 'phytosadism' of Harper 1985). Putz *et al.* (1984) found a significant correlation between the amplitude of crown- and branch-swaying in the wind and gap size in still air conditions in mangrove forests of *Avicennia germinans* in Costa Rica. Ng (1980) argued, however, that abrasion alone was not sufficient to account for the regularity of crown shyness observed in tropical rain forests of Malaysia. He suggested that, by detecting the changes in the light conditions around them, branch tips stop growing before any physical damage is produced. Since the existence of crown shyness is based on a subjective visual impression, deciding when this phenomenon occurs may be difficult in some circumstances. One might expect a whole range in the degree of 'shyness' of different species of trees. The results of the present study are interesting in this context because both kinds of crown interaction (abrasion and inhibition of growth) occur in different pairwise combinations of species. Three extreme outcomes are possible: (i) inhibition of the growth of both plants; (ii) inhibition of only one of them; and (iii) lack of inhibition of both members. Clearly, only the first of them will invariably produce crown shyness. The second case will normally be seen as the kind of hierarchy of shade-tolerant and shade-intolerant species. The last one will produce crown shyness only in cases where wind-swaying plays an important role in shoot mortality; otherwise the branches will tend to intermingle to some extent. The observation that crown shyness is common between members of the same species but not between members of different species may be due to a symmetrical response (either (i) or (iii) above) of the interacting trees or branches. This is, however, only a particular instance of the continuum of crown responses.

A similar phenomenon to crown shyness occurs in modular marine animals. Francis (1973 *a, b*; 1976) reports the agonistic behaviour of the sea anemone *Anthopleura elegantissima*. In this species clones can be produced by longitudinal fission of the individual anemones. When two clones of the same genotype meet, fusion between them is possible. When clones of two different genotypes meet, however, a strongly aggressive behaviour is elicited, involving the penetration by nematocysts of the tissues in close contact. This tissue becomes necrotic and the

damaged anemone may move or simply lean away from the aggressor. The result is something that looks very much like interclone 'shyness'. On a broader scale, Lang (1973) has reviewed the agonistic interactions between different species of corals. As in trees, the variety of interaction is not limited to 'shyness'. The presence of a 'pecking order' or hierarchy of species seems to be common.

The fact that each of the three conifer species studied showed differential response towards the other two raises the question of whether modules of a particular plant species are able to detect and respond differently to the presence of modules of the same and of different species. The term 'recognition' has been used to describe many different phenomena in both plant and animal studies (Heslop-Harrison 1978). In studies of animals it has mainly been used to describe the immunological identification by animal tissues of alien cells. This identification can involve two extremes in the amount of information and complexity required. On the one hand, the simple identification of self as opposed to non-self and, on the other, the specific recognition of, for example, a particular antigen. The simplest recognition mechanism, that of self and non-self, is common in colonial (modular) organisms (Burnet 1971). While modular animals are able to recognize the presence of genetically similar somatic tissues (Buss *et al.* 1985), in plants recognition seems to be restricted to the prevention of self-fertilization and, in horticultural practice, the restriction of the range of possible interspecific grafting.

One common characteristic of these recognition mechanisms is that they require the coupling of allosteric sites at the cell membrane level. The presence of a cell wall is obviously a strong physical impediment to the development of this capacity in plants. Very commonly, recognition at a distance occurs through the production and detection of chemical substances (Grant & Mackie 1974). This chemical recognition has been shown to be important in the detection and overgrowth of arborescent gorgonians by milleporid hydrocorals (Wahle 1980) providing a mechanism for the identification of space occupied by a competitively inferior species.

The kind of recognition to which we are alluding here is of a slightly different nature. It presumably involves changes in the physical (light) environment that could be detected by the photoreceptors of plants (although they also could probably act at the membrane level (Raven 1983)). Holmes (1983) has shown that plants can distinguish between the shade produced by other plants and the shade produced by inanimate objects. This distinction is possible through phytochrome detecting the increase in the ratio of red to far-red light underneath a live, green canopy.

Deregibus *et al.* (1985) have shown that tillering in *Paspalum dilatatum* and *Sporobolus indicus*, two common grass species of the Argentine Pampas, can be enhanced by artificially increasing the amount of red light underneath their closed canopies. Their results are reinforced by experiments with *Trifolium repens* by Solangaarachchi & Harper (1986), who grew plants of this species under three different amounts of photosynthetically active radiation: 100, 50 and 30% of incident light. For each of the two reduced levels of light, shade was produced by two different objects. In one case, pieces of black polythene floating in a water tank provided the canopy above the experimental plants. In the other, green leaves of *T. repens* floating in an identical water tank were used. Their results, for all the measures of plant performance recorded, are consistent with the hypothesis that at similar levels of photosynthetically active radiation a green canopy inhibits plant growth more than an inert canopy.

Holmes' (1983) argument is based on the importance to a plant of distinguishing between the shade cast by a neighbour plant and that produced by rocks or soil. In a highly competitive

environment, the importance of this recognition mechanism may rest more on the advantage of detecting when a taller neighbour has died so that stem extension rate can be rapidly modified, and the chance of access to the upper levels of the canopy improved. One could also hypothesize that the blue-light-absorbing photoreceptor (Briggs & Iino 1983; Holmes 1983) in conjunction with phytochrome may provide the plant with a more accurate picture of its surroundings.

Although different species have different degrees of response to changes in phytochrome photoequilibrium (Holmes 1983), the possibility of specific recognition of and response to broadly different kinds of shade cast by different species or groups of species with consequent modification of both extension rate of internodes and of module birth rate remains to be explored in greater detail.

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