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THE COMPETITION PROCESS IN FOREST STANDS

D. A. PERRY
Department of Forest Science, Oregon State University, Corvallis, Oregon, USA

I. INTRODUCTION

The design of cropping systems requires that we understand not only the physiology and genetics of individuals, but, because we grow plants in stands, also the nature of interactions among individuals. There are at least three reasons for this requirement. First, although high stocking densities reduce the growth of individuals, low stocking densities may under-utilize the site and therefore reduce yields; for a given combination of species and environment we must know how to balance these two factors. Second, competition has resulted in the evolution of a certain degree of resource allocation among individuals and species; more efficient land use may be achieved by understanding and exploiting such co-evolutionary relationships. Third, yields in genetically heterogeneous stands are likely to be better buffered against pests, pathogens, and climatic changes than those of genetically homogeneous stands; however, economic trade-offs between the short-term gains that we often associate with genetic homogeneity and the yield stability provided by genetic heterogeneity cannot be evaluated until we understand the genetic and environmental factors influencing plant community dynamics.

This paper is divided in two sections, 'Observation and experiment' and 'Theories and models.' In the first, I discuss what we know about the influence of competition on stand structure, the growth and form of individuals, and the growth of stands; I also deal with the ecology and genetics of competition – specifically, the question of resource allocation between species and between genotypes of the same species. In the second section, I briefly discuss some of the ways we go about organizing our observations into models and theories. I deal only with forests; for a discussion of agroforestry systems, see Cannell (1983).

II. OBSERVATION AND EXPERIMENT

'You can learn a lot by just looking' (Yogi Berra, famous American sportsman and philosopher).

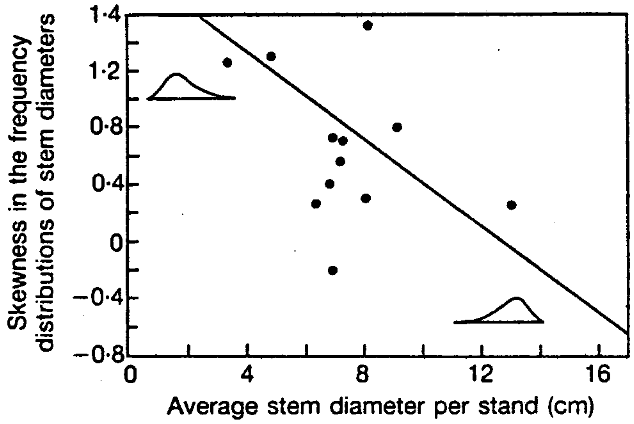

FIGURE 1. Relationship between average stem diameters and skewness of the diameter frequency distributions in 20- to 25-year-old *Pseudotsuga menziesii* stands in the Oregon Cascades (unpublished data). A similar relationship existed for average tree heights.

A. Competition and stand structure

Even-aged populations of most plant species follow a similar developmental pattern, which can be characterized by (a) the frequency distribution of individual plants sizes within the population, and (b) the relation between size of the average individual and stocking density.

In the early stages of stand development, plant weights are distributed normally, but with time the distribution becomes positively skewed or lognormal (ie has a preponderance of small plants, Ford 1975; Mohler *et al.* 1978; Kohyama & Fujita 1981). Diameter and height distributions may move from normal to negatively skewed before eventually becoming positively skewed (Gates 1982). Skewness in the diameter distributions of *Pinus radiata* plantations studied by Gates *et al.* (1983) changed from 0 (normal) to negative and back to positive within 25 years. In 20- to 25-year-old *Pseudotsuga menziesii* stands in the Oregon Cascades, diameter and height distributions tend to positive skewness in stands with relatively small trees and to become progressively more negatively skewed as the average tree size increases (Fig. 1; actual distributions in these stands are shown as insets in Fig. 5). Apparently, rapid early growth by a few individuals (sprinters) in each stand establishes the early positive skewness, but as slower early growers (stayers) catch up the distribution becomes negatively skewed.

It is not necessary to invoke competition to explain the characteristic lognormal size distribution of plant populations: it results from exponential growth of individuals within initially normally distributed populations (Koyama & Kira 1956; Koch 1966). However, competition is likely to reinforce and perhaps to magnify any hierarchy in plant sizes. When mortality reaches about 50%, a bimodal distribution may develop which probably indicates that 'one-sided' competition has occurred – ie large trees have suppressed smaller ones, but small trees have competed very little with larger ones (Ford & Newbould 1970, 1971; Ford 1975). One-sided competition occurs where light is the primary limiting factor (Ford & Diggle 1981); where water and nutrients also are limiting, competitive interactions may become more symmetric.

As competition intensifies during stand development, suppressed plants eventually die, and 'self-thinning' begins. Usually, a constant proportion of the total plants die in any given time period, so that plant numbers decrease exponentially with time, but Kohyama and Fujita (1981) found that, as stands aged, a decreasing proportion of trees died in subalpine *Abies* forests of Japan.

Once self-thinning has begun, the relationship between average plant size and stocking density is characterized by the self-thinning 'law' (reviewed by White 1980; Westoby 1984), stated mathematically as:

$$\log \bar{w} = c - x \log \rho \qquad (1)$$

where $\bar{w}$ is the average plant size (eg weight or volume), ρ is the stocking density, and c and x are constants. The line described by equation 1 represents a ceiling on average plant size at any given stocking density. When a population is self-thinning, any increase in individual plant size is accompanied by a decrease in stocking density; the resulting trajectory, a negatively sloped straight line when expressed on a log-log scale, is the self-thinning line.

The self-thinning law has two remarkable properties. First, although the intercept and slope of the line vary among species, the magnitude of variation is quite small. In White's (1980) tabulation of 36 species, ranging from annuals to trees, slopes (x) varied between $-1{\cdot}30$ and $-1{\cdot}80$ (with most between $-1{\cdot}4$ and $-1{\cdot}6$), and intercepts (c) varied between 3·06 and 4·41. Second, within a given species, there seems to be little site-related variation in the intercept and slope of the self-thinning line. The only significant exception detected so far is that shading can lower the slope of the line.

The intercept of the self-thinning line may tell us something about competitive interactions. For instance, tree species with narrow crowns tend to have larger intercepts than those with spreading crowns (Harper 1977), suggesting that more narrow- than broad-crowned trees of a given size can be packed on to a piece of ground – a very logical proposition.

The slope of the self-thinning line reflects the relationship between mortality and the growth of surviving trees, a steeper (more negative) slope indicating greater growth per unit of mortality than a shallower slope. 'Greater growth' may mean either more total biomass added or more biomass allocated to the plant part measured, such as the bole. Change in total biomass with density may be quite different from that in any single biomass component, and the various biomass components may, in turn, differ from each other (Mohler *et al.* 1978; Hutchings 1979). Self-thinning lines based on leaf weight tend to have slopes close to −1·0, which is appreciably shallower (less negative) than those of lines based on total biomass or other biomass components (Mohler *et al.* 1978; Hutchings & Budd 1981). This difference reflects the fact that the maximum leaf area on a given site may be reached relatively early in the self-thinning process; thereafter, although total stand biomass continues to increase, total leaf biomass remains constant (Long & Smith 1984).[1]

What does the slope of the thinning line tell us about the competition process? It is tempting to argue that the growth increment accompanying mortality is a response to reduced competition, and that steeper (more negative) thinning lines reflect more intense competition. However, by the time a suppressed individual dies, its passing is likely to be little noticed by surviving dominants (Ford 1975). West and Borough (1983) demonstrated this fact for stands of *Pinus radiata*, whose self-thinning lines have slopes approaching −1·5 only if suppressed individuals are counted as mortality.

In my opinion, the self-thinning trajectory has a great deal to tell us about the dynamics of the competition process; and the message must be read, as all of nature's ciphers, by a combination of theory and experiment through which the underlying dynamic processes are unravelled.

B. Effect of competition on individual tree growth

Competition influences both the growth of individuals and how this growth is distributed. Much of the direct effect of competition on growth is mediated through its impacts on (a) the amount of carbon fixed per unit leaf area, and (b) crown size and structure. It is well known in agriculture that net assimilation rates (NAR, dry matter production per unit leaf area) decline with increase in leaf area index (LAI); Figure 2 shows this effect for stemwood production of various forest stands in Washington state (Schroeder *et al.* 1982).

As a stand approaches full leaf area, branch production is reduced, and self-pruning causes the base of the crowns to shift upwards (eg Cochrane & Ford 1978). Because of increased internal shading, branch mortality may be greater on large trees than on small ones (Oker-Blom & Kellomäki 1982). Bole increment is often greatest at the crown base (Hall 1965; Brix 1983);

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[1] A self-thinning slope of −1 means that the weight of an individual changes with density such that the *total* stand weight remains constant. Slopes steeper (more negative) than −1 reflect an increase in total stand weight during self-thinning.

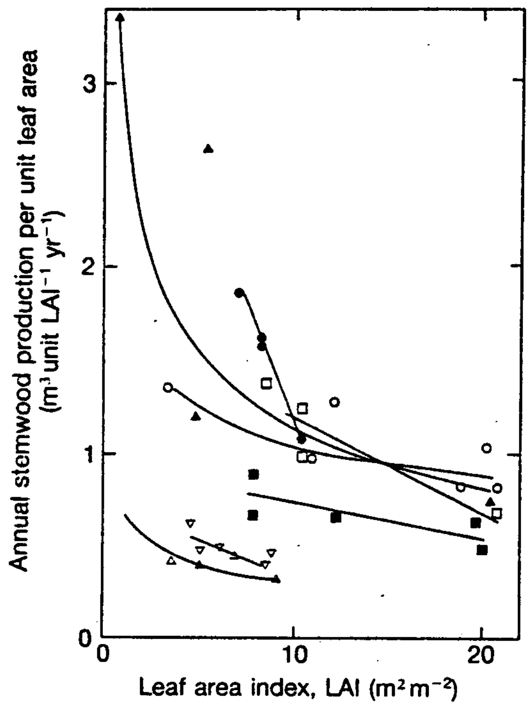


FIGURE 2. Relationship between (a) stemwood production and (b) leaf area index, in seven conifer stands in eastern Washington (from Schroeder *et al.* 1982).

therefore stem form is likely to be altered during this process as well. Ford (1982) found that the onset of competition in a *Picea sitchensis* plantation was accompanied by a decline in both stand productivity and projected needle area index (from 10–11 at age 16 to 7–8 at age 18).

Trees, like other plants, can compensate somewhat for shading. Shade leaves of *Castanea sativa* have greater surface/weight ratios and more chlorophyll per unit weight than sun leaves (Ford & Newbould 1971). Kellomäki and Hari (1980) found that trees in the lower social positions of *Pinus sylvestris* stands had greater height and radial growth rates than dominants, at least partially because of lower respiration rates and higher leaf area/leaf weight ratios.

What about the trees that are winning the competitive race? Their crowns become larger and broader, which means they accumulate more photosynthetic machinery and are able to fix more carbon. However, respiration by the infrastructure of stems, branches, and roots that accompanies larger crowns usually means decreasing productive efficiency. Maintenance respiration by large trees may be much greater than indicated by studies of woody respiration on small trees, which are relatively efficient at recapturing respired carbon (Waring & Schlesinger 1985). Rook and Carson (1978) found that the respiration rates per unit area of the lower bole of a seven metre tall *Pinus radiata* tree were four times greater than those of an equal surface area of leaves.

Assmann (1970), reviewing European research on coniferous and deciduous tree species, concluded that, within any given social stratum, trees with small- to medium-sized crowns have larger wood increments per unit crown (or ground) surface area than trees with large crowns. The improved light environment of the emerging dominants, however, tends to offset declines due to greater respiration. For instance, in *Pinus sylvestris* plantations there is only a small decline in wood increment per unit crown surface area with increase in tree size among dominant trees, whereas there is a very sharp decline among codominant and dominated trees (Fig. 3). Mayer (1957, cited in Assmann 1970) showed similar relationships in *Quercus petraea* stands.

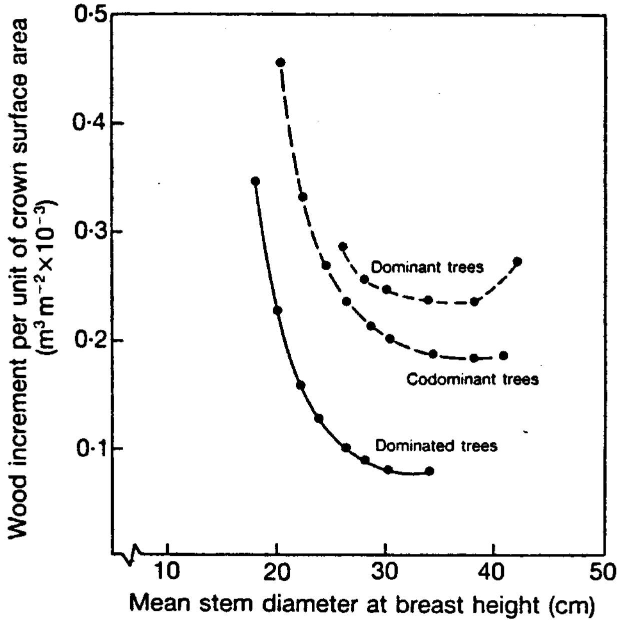


FIGURE 3. Change in wood increment per unit of crown surface area with increasing stem diameter at breast height, for trees in three social classes within *Pinus sylvestris* plantations (adapted from Assmann's 1970 summary of Badoux 1945).

Trees in thinned stands respond in much the same way as emerging dominants in unthinned stands. The needle/branchwood weight ratio was 1·50 in thinned *Pinus contorta* stands, compared with 2·36 in unthinned stands (Gary 1978), so that the latter had nearly 60% more photosynthetic tissue per unit of respiratory tissue. Trees in 43-year-old *Pseudotsuga menziesii* stands planted at close spacings had larger ratios of crown surface area to crown volume than trees planted at wide spacings (Curtis & Reukema 1970; Fig. 4). Volume increment per unit of crown surface area was 22% greater in heavily thinned than in densely stocked stands of *Picea abies* (Burger 1939, cited in Assmann 1970), but, when increment was measured per cubic metre of crown exposed to direct light, efficiency in the densely stocked stand was nearly twice that in the thinned stand.

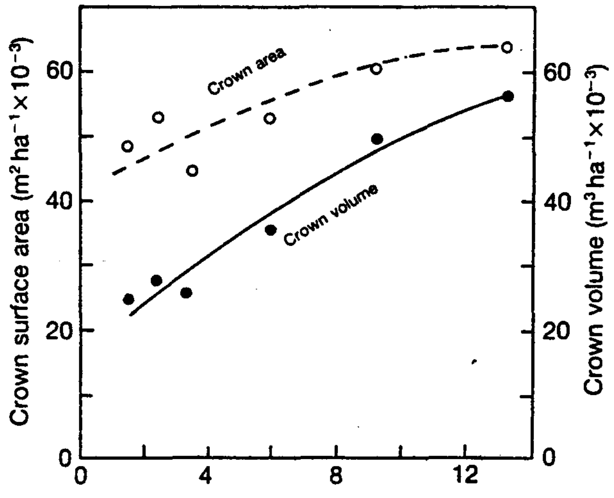


FIGURE 4. Crown surface areas and crown volumes of trees in 43-year-old *Pseudotsuga menziesii* stands planted at different densities (adapted from Curtis and Reukema 1970).

Despite the range of plastic responses available to dominated trees, high levels of competition reduce growth. Relative growth rates (RGRs) decline sharply with decreasing social status in *Picea sitchensis* (Ford 1975) and *Pinus radiata* (West & Borough 1983) plantations. Figures 5A-D (unpublished data) show the relation between competition levels and the RGRs (2-year basal area growth relative to basal area at the start of the 2-year period) of trees in various size classes in four *Pseudotsuga menziesii* stands in the Oregon Cascades. All are about 20 years old and are mixtures of planted and natural trees. Plots in each stand were thinned three years before measurement, to leave a range of size classes. Competitive levels in unthinned plots were measured as relative density (RD), or stocking density relative to the maximum theoretically attainable at a given mean stand diameter at breast height, the latter taken from Reineke's (1933) maximum density line for *P. menziesii*.

Unthinned plots of the stand shown in Figure 5A have an average RD of 0·22; competition is not severe enough to produce competition-related mortality, small trees have larger RGRs than large ones, and thinning produced no 'release' – ie, despite the strong positive skewness of diameters (inset), no size class is suppressed. The stand shown in Figure 5B is probably in the early stages of competition-related mortality (RD = 0·54). Diameters are negatively skewed, but RGR differs little among social classes and responds only slightly to thinning. Note that diameters are distributed normally in this stand. As I suggested earlier, the greater growth efficiency (larger RGRs) of small trees enables them to catch up with fast early growers. In the stand shown in Figure 5C (RD = 0·75), trees in the lower diameter classes are clearly suppressed and respond strongly to thinning. Note, however, that the RGR

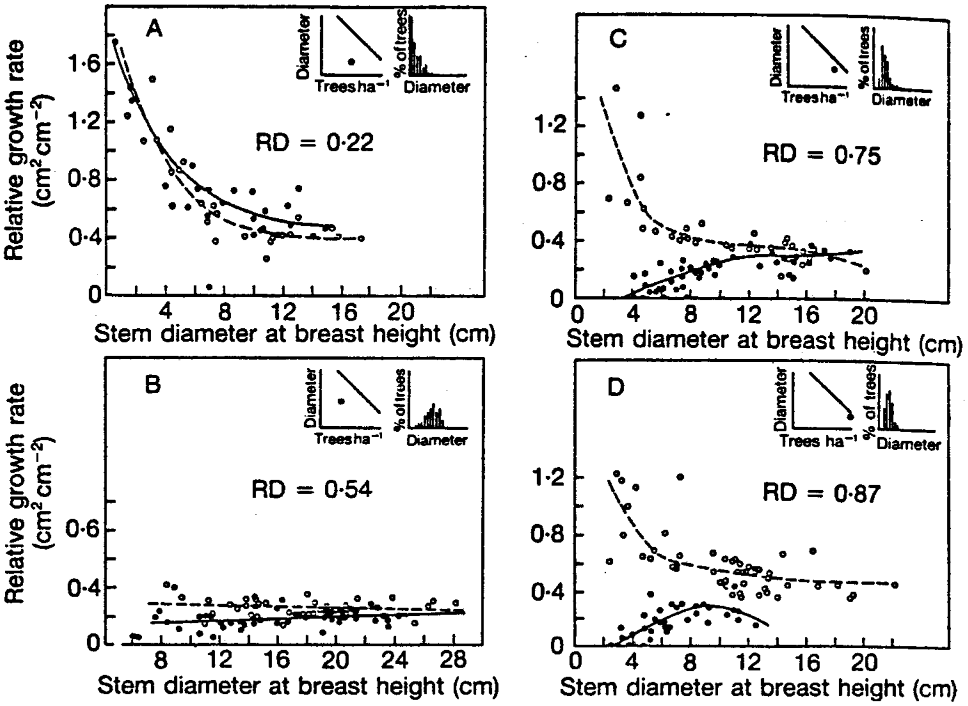


FIGURE 5. Relative growth rates (RGRs) of *Pseudotsuga menziesii* trees of different stem diameters in thinned (open circles and dashed lines) and unthinned (closed circles and solid lines) plots in four stands of different 'relative densities' (RDs); thinned plots were cut three years before measurement.

RGR = basal area growth over the past two years relative to basal area at the start of the two-year period; RD = actual stocking density relative to the theoretical maximum. Insets show, for the unthinned plots, the diameter-density point relative to the theoretical maximum stocking density (Reineke 1933) and the diameter frequency distributions. The scales on the insets are: 0–20 cm diameter (DBH), 0–8100 trees ha^{-1} and 0–40% of trees.

of trees larger than 12 cm in diameter does not increase following thinning, a clear example of one-sided competition. The stand shown in Figure 5D (RD = 0·87) is probably experiencing competition-related mortality, and manifests the same pattern of suppression in the lower size classes as the stand in Figure 5C. The response to thinning in Figure 5D suggests that, under these superdense conditions, the growth of larger, as well as of smaller, trees may have been reduced; however, stand density before thinning was not as high in the thinned as in the unthinned plot of this stand, so the interpretation is confounded.

Cannell *et al.* (1984) reported changes similar to those shown in Figure 5 in RGR patterns for height in stands of *Pinus contorta* and *Picea sitchensis*. RGR was initially negatively correlated with tree height (cf Fig. 5A), but, as competition intensified, the correlation became positive (cf Figs 5C, D).

C. Environment and competition

The environment can have profound, and surprising, effects on the competition process. This fact may be illustrated by differences in the response to thinning of 15- to 20-year-old stands of *Pseudotsuga menziesii* growing in varying topographic positions in the Oregon Coast Range (Perry, unpublished). Whereas the RGR of trees growing on steep slopes (50–80%) increases after thinning, RGR actually decreases after thinning on shallow slopes! There are several plausible hypotheses that may explain this phenomenon, including thinning 'shock', increased root rot, decreased mycorrhizal formation, and high water tables. The evidence supports the last hypothesis – that is, the removal of leaf area results in decreased evapotranspiration, a rise in the water tables, and a subsequent reduction in tree growth. Clearly, we must be very careful when extrapolating competitive interactions from one environmental setting to another.

D. Crown characteristics and competition

The fact that dry matter production per unit leaf area (net assimilation rate, NAR) is a trade-off between photosynthesis and respiration suggests that the degree of competition among individuals, at a given stocking level, depends on their crown characteristics. A simple model illustrates this point. Assume that:

$$\mathrm{NAR} = \frac{P}{\mathrm{LAI}} - R \qquad (2)$$

where P is gross photosynthesis per unit leaf area in the absence of competition, LAI is leaf area index, and R is respiration per unit leaf area. As noted earlier (Fig. 2) NAR is inversely related to LAI. It is assumed that R is independent of LAI.

Consider two hypothetical stands (Fig. 6), both with gross photosynthetic rates (P) of $40\,\mathrm{g\,m^{-2}\,day^{-1}}$, but one consisting of large-crowned individuals with a base respiration rate of $10\,\mathrm{g\,m^{-2}\,day^{-1}}$, the other of small-crowned individuals with a respiration rate of $5\,\mathrm{g\,m^{-2}\,day^{-1}}$ (these numbers are arbitrarily chosen). At any given leaf area, the small-crowned individuals have larger NARs than the large-crowned ones, and, though the absolute difference between the two is a constant $5\,\mathrm{g\,m^{-2}\,day^{-1}}$ (the difference in respiration rate), the relative difference between them increases with increasing LAI. Now, suppose we thinned the small-crowned stand from LAI 4 to 2 (Fig. 6, points A to B). NAR would initially increase, but, as the stand returned to full site occupation (measured by LAI), the NAR would shift toward that of the large-crowned trees. By the time the original leaf area was regained (point C), the trees would, of course, be larger, but they would have smaller NARs than before thinning.

Brix (1983) may have seen this effect in thinned and fertilized plots of *Pseudotsuga menziesii*. Plots were treated in 1970; within one to two years stemwood production per unit leaf area was 30%, 78%, and 135% greater than that of controls in thinned, fertilized, and thinned and fertilized plots,

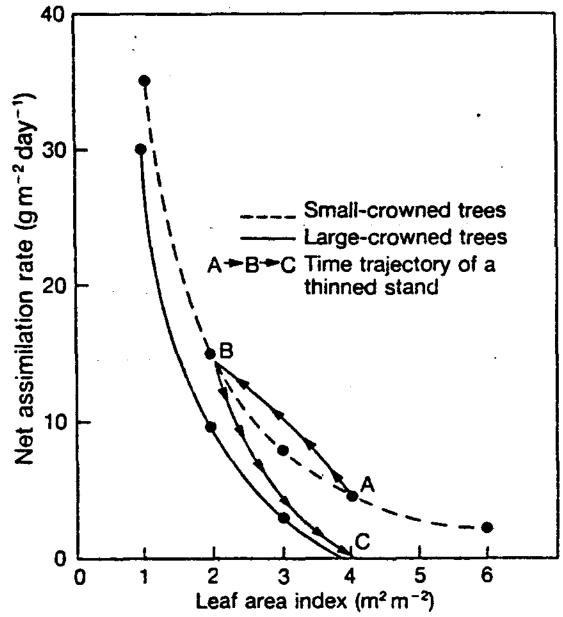


FIGURE 6. Hypothetical relationships between net assimilation rates and leaf area indices for two stands composed of trees with small or large crowns (see text).

respectively. However, stemwood production per unit leaf area subsequently decreased, and by 1977 was at least 20% below that of controls in all treatments. Unfortunately, Brix's data do not allow LAIs to be calculated, so the reason for the decline in stemwood production per unit leaf area cannot be clearly identified.

E. Effects on carbohydrate allocation

Competition has important influences on carbohydrate allocation and tree form other than its effects on crowns. It is a conventional wisdom in forestry that growth in stem diameter is more affected by changes in stand density than growth in tree height. In *Picea sitchensis*, the most dramatic effects on height/diameter ratio occur at the highest initial stocking levels (Jack 1971). Assmann (1970) found that differences in height/diameter ratio among *Picea abies* stands, thinned to different levels, increased with age to a certain point, beyond which they tended to disappear. Thus, competition altered the temporal pattern, rather than the absolute amount, of height relative to diameter growth.

Species differ in the relative response of height and diameter growth to competition. Height growth of *Pinus contorta*, for example, is very sensitive to stocking density (Holmes & Tackle 1962), whereas that of *Larix occidentalis*, its close ecological associate, is little affected (Seidel 1977). In *Pseudotsuga* *menziesii* stands, trees within the same social class differ greatly in height/diameter ratio, suggesting that considerable genetic diversity exists within species. As I shall discuss later, genotypes within the same population differ in their response to competition.

Competition can influence the chemical composition of trees. Lower photosynthesis probably results in reduced allocation of photosynthates to those chemical constituents that are most energy-expensive. This effect is likely to differ with species, site, and season, but a rough idea of priorities can be gained from the grams of glucose required to synthesize one gram of various compounds in *Pinus taeda*: lipids, 3·02 g; phenolics, 1·92 g; lignin, 1·90 g; nitrogenous compounds, 1·58 g; organic acids, 1·43 g; and carbohydrates, 1·13 g (Chung & Barnes 1977). The more expensive compounds include important defensive chemicals, such as terpenes and tannins, which have lipid or phenolic precursors. Density stress does, at least in some cases, increase tree susceptibility to insect herbivores (Mitchell *et al.* 1983).

The production of fruits and seeds is likely to be curtailed by stresses of any kind. Flower bud production is sharply reduced by shading in most fruit trees (Cannell 1983; Jackson, this volume). Seeds of some species, such as *Acer saccharinum*, *Quercus rubra*, *Pinus strobus*, and *Pinus palustris*, contain a high proportion of energy-expensive fats and/or proteins (Kramer & Kozlowski 1979); thus, unless the situation becomes so severe that stress-related seed crops are produced, seed production may well be one of the first things sacrificed when resources are scarce.

F. The ecology of competition

1. *Stand structure and 'competitive tension'*

When we talk about, or attempt to define, competitive interactions, we invariably refer to effects on individuals, but there are also system-level implications. One of the robust general principles of plant ecology is the law of constant final yield – better known in forestry as Langsaetter's relation – which simply states that over a wide range of stocking densities total yields are the same (Kira *et al.* 1953; Harper 1977). Various caveats accompany this statement, including the fact that it is not consistent with the self-thinning law; nevertheless, if we are careful about the time frame within which yields are compared, it is reasonably accurate.

At high plant densities, mutual interference can decrease community yields: this is what foresters call stagnation. But most plant communities do not stagnate because the development of a dominance hierarchy effectively dissipates 'competitive tension' – a process much like that in non-equilibrium thermodynamic systems, where structure is created and maintained by the dissipation of energy (Prigogine 1980). Thus, the competition process, through the heterogeneous stand structure it produces, may play a positive role when veiwed in the context of the community. Wood production per unit leaf area in Amazonian forests, for example, is greatest in those stands with the most complex, aerodynamically rough, canopies (Brunig 1983). It is possible that the decline in LAI and productivity sometimes seen in rapidly growing young conifer plantations (Ford 1982) is due to a build-up of 'competitive tension' resulting from inadequate expression of dominance.

2. *Resource allocation among species*

Plants share the same basic resources and therefore would seem to have fewer options for niche separation than animals, although Tilman (1982) has pointed out that there are far more plant species per limiting 'plant resource' than animal species per limiting 'animal resource'. Most plant species diversity is due to small-scale environmental heterogeneity (Harper 1977), although both the canopy and rooting zone can be vertically stratified (Trenbath & Harper 1973; Yeaton *et al.* 1977). Of the numerous studies of species mixtures, relatively few have found that yields of mixed species differ significantly from those of pure stands (Trenbath 1974). However, most of these studies have looked at plants of similar stature which share environmental resources over the same time frame (see Cannell 1983). Harper (1977) pointed out that most (a) were conducted in pots with inadequate soil volumes to allow root separation, and (b) used agronomic species bred to grow in low-density monocultures. I would add that they used artificial soil media containing neither the structure nor the microbial richness of natural soils.

Harper (1977) stated that 'a search for "ecological combining ability" is most likely to be successful in species or varieties that have been specifically bred for or evolved naturally toward some degree of niche separation'. But few studies of combining ability in nonagronomic species have been conducted; therefore, our understanding of the relationship between structure and productivity in natural systems remains minimal.

Parrish and Bazzaz (1982) found that species from a late successional community had greater 'ecological combining ability' than species from an early successional community. Turkington *et al.* (1977) showed that different legumes formed consistent relationships with certain grass species within Ontario grasslands, suggesting that selection had occurred for species-specific neighbours. Both Assmann (1970) and Braathe (1957), reviewing European experience, concluded that mixing shade-tolerant and shade-intolerant trees often resulted in greater productivity than when intolerants were grown alone; in one series of experiments the yield of *Pinus sylvestris-Fagus sylvatica* mixtures was up to 24% greater than that of pure *P. sylvestris* (Assmann 1970). The same seems true of *Pseudotsuga menziesii-Tsuga heterophylla* mixtures in the Pacific Northwest (Wierman & Oliver 1979). The relative advantage of mixtures is likely to vary with site; for instance, the ability of a single species to dominate and exclude others can be greater at high than at low fertility levels (Austin & Austin 1980), and soil pH is an important determinant of yield in *Fagus sylvatica-Picea abies* mixtures (Assmann 1970). Stand factors also can be important; Vandermeer (1981) showed that, theoretically, the yield of species mixtures relative to monocultures depends on the density at which plants are grown.

In some instances, species packing is increased within plant communities through 'mediators' such as grazers, pathogens, pollinators, or symbionts which act selectively (eg Burdon & Chilvers 1974; Yodzis 1976; Hanley & Taber 1980). The most striking and consistent examples of increased yield in mixtures relative to monocultures are those involving nitrogen-fixing species. When de Wit *et al.* (1966) grew *Panicum maximum* with the legume *Glycine javanica*, they found transgressive behaviour (increased yields in mixtures) only when *Rhizobium*, the nitrogen-fixing symbiont of legumes, was added. Thus, niche separation between the plant species was mediated by the bacterium. Binkley (1983) found that *Pseudotsuga menziesii-Alnus rubra* mixtures were more productive than pure *P. menziesii* stands in soils low in nitrogen, but in soils less limiting in nitrogen this was not the case. In general, where a symbiont can both decrease competition for some limiting factor and act symmetrically (not at the expense of one species), transgressive yields may result. Bowen (1973, 1980, and this volume) suggested that ectomycorrhizas enabled sparsely rooting species, such as trees, to compete more successfully with intensely rooting species, such as grasses, which are not ectomycorrhizal. In that case, alteration of competition by the symbiont (the mycorrhizal fungus) is presumably asymmetric, because trees gain at the expense of grasses. However, if the ectomycorrhizas released organic acids which accelerated solubilization of mineral elements (Graustein *et al.* 1977) or increased the level of antibiosis in the soil, then benefits could conceivably accrue to non-ectomycorrhizal as well as to ectomycorrhizal plants, and competition would become less asymmetric.

3. *Intraspecific competition*

Donald (1968) recognized that stands of less aggressive 'crop' ideotypes were likely to yield more than stands of 'isolation-competition' ideotypes, and the widespread introduction of the former was an important part of the Green Revolution. Ford (1976) and Cannell (1978) have argued the advantages in forestry of using 'crop' ideotypes, which utilize space efficiently and therefore have high yields per hectare in stands. In this section, I deal with a different aspect of the genetics of competition, the allocation of resources among genotypes of a single species.

Intergenotypic competition is probably the most understudied aspect of forest growth dynamics (Libby *et al.* 1969; Adams 1980). Yields in pairwise varietal mixtures of agronomic species are generally either complementary (yield reduction by one variety is balanced by gains in the other) or overcompensatory (yield in mixture is greater than the mean yield of the two monocultures) – which is remarkable, considering that agronomic varieties are bred for high individual yields (or at least were at the time most experiments were conducted), and have no history of co-evolution (see Adams 1980).

One approach to studying intergenotypic competition in forests has been to compare clonal with mixed-genotype stands (Sakai & Mukaide 1967; Sakai *et al.* 1968; Hühn 1969, 1970). Sakai *et al.* (1968) suggested that competition was less in a clonal than in a mixed-genotype forest, but they defined competition as a reduction in the growth of one individual relative to a neighbour, which leads to the absurd conclusion that little competition exists in a stagnated stand. A more relevant measure of competition is growth relative to an open-grown standard (eg Riitters 1985), or growth within a replacement series, in which the proportions of competing genotypes are varied while the total numbers are held constant (de Wit 1960).

I am aware of only three experimental tests of ecological combining ability among genotypes within a single tree species. Adams *et al.* (1973) tested all pairwise combinations of four *Pinus taeda* families; four combinations produced overcompensation, four complementation, two neutrality (no difference between the growth of either genotype in mixture or monoculture), and two undercompensation (the mixture yielded less than the mean yield of the monocultures). There was evidence in this study that related genotypes (half-siblings) were competitively neutral. Adams and Demeritt (unpublished, cited in Adams 1980) found that mixtures of hybrid *Populus* sp. clones were either overcompensatory (2 of 15 pairs), complementary (4 of 15), or neutral. Tauer (1975) showed similar relationships among clones of *Populus trichocarpa*.

With the exception of Adams *et al.* (1973), these studies suffer the same limitation as experiments with agronomic plants: they deal with genotypes which have had no co-evolutionary history. If ecological combining ability is found in even a small percentage of randomly combined clones, the probability is high that it is a significant factor in the growth of natural forests (cf Adams 1980; Hühn 1973). There is evidence supporting this view; the growth of genotypes in stands is often poorly correlated with their performance in the open (Franklin 1979; Panetsos 1980), and half-sibling families of several tree species have been shown to differ greatly in their response to density stress, particularly in shoot growth and shoot/root ratios (Fig. 7; Malavasi and Perry, manuscript in review).

Theoretically, evolution will favour stable mixtures of genotypes which differ in competitive ability only if there is some degree of overcompensation (ie resource allocation) in their competitive interactions (Schutz *et al.* 1968; see also Stern 1969). The selective forces pushing plant populations toward resource allocation are sometimes quite strong. This point was illustrated by Allard and Adams (1969), who showed that wheat cultivars grown in mixtures for eighteen generations evolved so that they yielded better in mixed stands than in monocultures. In my opinion, and particularly in view of our current fascination with clonal forestry, research into the extent and nature of intergenotypic interactions should be given high priority.

III. THEORIES AND MODELS

'To give an accurate description of what has never occurred is . . . the inalienable privilege of any man of parts and culture' (Oscar Wilde).

A. The self-thinning rule

Theories of the self-thinning rule fall into two general categories: those based strictly on allometry, and those including both allometry and physiology. In their original derivation of the $-3/2$ slope, Yoda *et al.* (1963) simply divided space according to certain rules, namely that: (a) plant weight is a cubic function of some linear plant dimension such as diameter (or height is linearly related to diameter), (b) plant geometry remains constant during self-thinning,

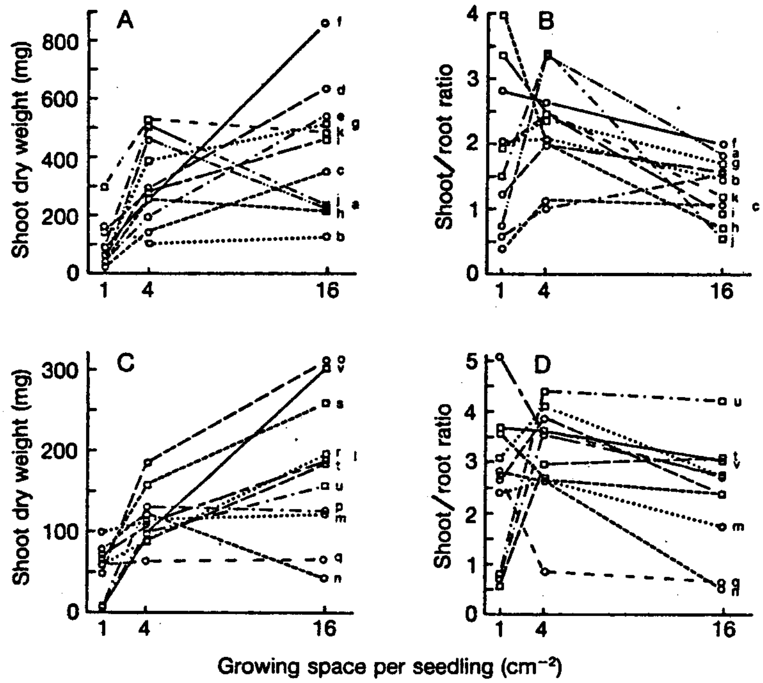


FIGURE 7. The differing responses, in shoot weight and shoot/root ratio, of one-year-old seedlings of half-sibling families (denoted by different letters) of *Pseudotsuga menziesii* (A and B) and *Tsuga heterophylla* (C and D) to density stress (from Malavasi and Perry, manuscript in review). Seedlings were grown in shade frames at Corvallis. Similar differences were found among half-sibling families of *Abies nobilis* and *Abies amabilis*. All family-density interactions except those for *P. mensiesii* shoot weights (A) were significant at the 0·01 level.

(c) increases in plant size are linearly related to increasing increments of growing space, and (d) the reciprocal of population density is an accurate estimate of the growing space available to the average tree. Various authors have pointed out the inaccuracies of these assumptions (Ford 1975; Mohler *et al.* 1978; White 1981). White (1981) mustered a great deal of data to show that the relationship between height and diameter in trees is rarely linear, and that the relationship between biomass and diameter is not cubic. He used the following allometries:

$$W \propto d^{2\cdot5} \text{ and } C_D \propto d^a$$

where W is individual tree biomass, d is stem diameter at breast height, C_D is crown diameter, and a is a constant, to derive:

$$W \propto \rho^{-2\cdot5/2a} \qquad (3)$$

where ρ is stocking density. Equation (3) predicts that trees with wide crowns in relation to stem diameter (ie large values of a) thin along a shallower (less negative) slope than trees with narrow crowns.

An alternative, slightly more general, derivation is based on the following allometries (Perry, unpublished):

$$h \propto G_A^Q \text{ and } W \propto E_V^Z$$

where h is tree height, G_A is ground area per tree, E_V is environmental volume per tree ($= G_A \times h$), and Q and Z are constants. These give:

$$W \propto \rho^{-Z(Q+1)} \qquad (4)$$

where Q measures tree height in relation to ground area (the reciprocal of density), and Z above-ground biomass in relation to the environmental volume that a tree occupies. Values less than 1 for either parameter indicate 'diminishing returns' as the tree gains more space.

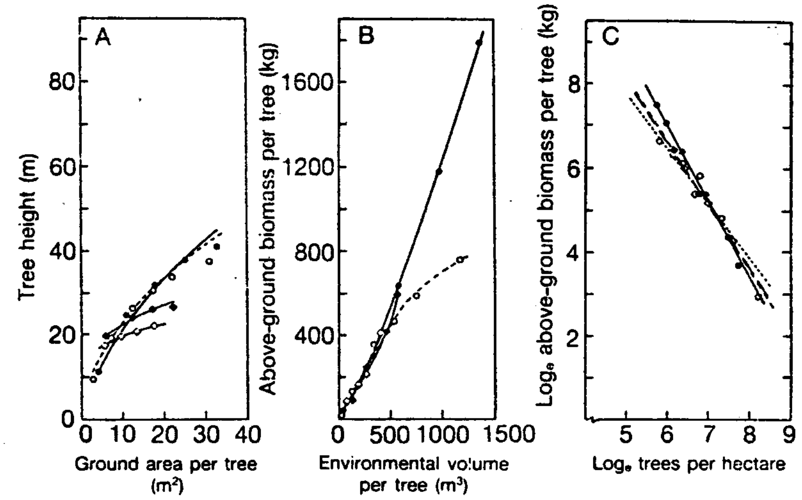


FIGURE 8. Effect of A. tree height in relation to ground area per tree and B. above-ground tree biomass in relation to the environmental volume occupied per tree (ground area×height) on the slope of the self-thinning line C.

Closed circles: *Pseudotsuga menziesii*: good site (52 m tall at age 100); open circles: poor site (42 m tall at age 100). Closed diamonds: *Pinus ponderosa*: good site (36 m tall at age 100); open diamonds: poor site (24 m tall at age 100).

The *P. menziesii* data were taken from McArdle and Meyer (1961), the *P. ponderosa* data were adapted from Oliver and Powers (1978), and biomass values were calculated from the stem diameters using regressions given by Gholz *et al.* (1979).

Figure 8 illustrates how variation in Q (tree height vs ground area per tree) and Z (above-ground biomass vs environmental volume per tree) affects the slope of the self-thinning line of *Pseudotsuga menziesii* and *Pinus ponderosa*. Height is roughly equal to the square root of ground area per tree for *P. menziesii* but not for *P. ponderosa*. The relation between biomass per tree and its environmental volume (ground area× height) is a nonlinear power function for *P. menziesii* on good sites (52 m tall at age 100) and for *P. ponderosa* on both good (36 m tall at age 100) and poor (24 m) sites; but *P. menziesii* on poorer sites (42 m) is fit more closely by the monomolecular equation $(1-e^{cE}V)$, where c is constant. Despite very different values of Q for *P. menziesii* on the poorer sites and *P. ponderosa* on the better sites, the slope of the self-thinning line for the two is the same because *P. ponderosa* occupies increasing growing space more efficiently (ie has a relatively high Z value). *P. menziesii* on good sites has high values of both Q and Z and therefore a self-thinning slope more negative than $-1{\cdot}5$.

Because the efficiency with which a tree occupies space is a function of both its geometry and physiology, theories incorporating both are likely to give the clearest insight into the mechanisms underlying self-thinning. I am aware of only two such theories. Pickard (1983) used elementary relations between available photosynthate and either total plant or crown size in three different approaches, all of which gave slopes close to $-3/2$. Perry (1984) derived a self-thinning relation from Richards' generalized Von Bertallanfy equation (a logistic equation relating growth to photosynthesis and respiration; Richards 1959) which generates some fairly specific and testable hypotheses. For example, for intercepts to be produced within observed ranges, the rate of carbon loss from individuals (maintenance respiration, tissue death, etc) must exceed the individual mortality rate. The model further predicts that the self-thinning slope is determined jointly by the allometric relation between total above-ground biomass and leaf area and by photosynthetic tolerance to density; plants which maintain relatively high leaf areas as they enlarge have relatively steep thinning slopes, and tolerant plants have relatively shallow slopes. These two factors are generally not independent – tolerant plants tend to maintain relatively high leaf areas and *vice versa*; therefore, according to this model, feedback between plant allometry and physiology constrains the self-thinning slope within a relatively narrow range.

B. Individual tree models

The role of competition in stand structure and growth is most often modelled as the simple linear sum of competitive interactions between individuals. Clearly, the essential ingredient in this approach is an algorithm which successfully predicts how the growth of an individual is influenced by its neighbours. There are two ways to go about formulating such an algorithm; the more direct is to correlate the growth of an individual with some combination of distance to, and size of, its neighbours; the other is to assume logistic growth toward a competition-dependent maximum, for example the self-thinning line or some measure of growing space.

1. *Distance-size models*

Numerous 'competition indices' have been used in attempts to quantify the influence of neighbours on tree growth. These can be grouped according to the way in which competition is calculated (cf Adlard 1974; Alemdag 1978). Competition can be calculated from: (a) neighbour encroachment into an 'optimum growing space', which is generally defined as the open-grown crown diameter (eg Bella 1971; Gates 1982); (b) the basal area of neighbours (Opie 1968); (c) the available growing space calculated as a polygon, with vertices dependent on the spatial arrangement of neighbours (eg Adlard 1974); (d) the diameters and distances of neighbours (Hegyi 1974); (e) crown surface, volume, etc, in relation to open-grown trees (eg Mitchell 1975); and (f) relative plant sizes or heights, but with competition effects one-sided, that is with trees below a certain relative size having little or no competitive effect (eg Gates 1978; Ford & Diggle 1981).

In general, competition indices by themselves explain a disappointingly small proportion of variation in tree growth, even in stands occupying uniform sites (eg Alemdag 1978; Noone & Bell 1980). Invariably, the most important predictor of how a tree is growing is its own size, independent of its neighbours. Four reasons for this fact come to mind. First, past competitive interactions are integrated in current tree size. Second, variability is introduced because of genotypic differences in response to competition, and because of environmental heterogeneity (cf Cannell *et al.* 1977). Third, as discussed earlier, interactions between individuals can be co-operative rather than competitive. And fourth, where light is limiting, indices based on two-sided competition may not accurately reflect the competition process; in fact, one-sided models have been successful in reproducing the bimodal size distributions which characterize populations with strong dominance hierarchies (Diggle 1976; Ford & Diggle 1981; Gates 1978, 1982).

2. *Logistic-type models*

Logistic growth is simply exponential increase damped by some limiting factor. Of the various ways of writing a logistic equation, one of the more general is:

$$\frac{1}{B}\frac{dB}{dt} = \frac{r(t)}{a}\left[1 - \left(\frac{B}{K(t)}\right)^{a}\right] \tag{5}$$

where B is some measure of size, such as biomass, $K(t)$ is the maximum attainable B, $r(t)$ is an 'intrinsic' growth rate, and a is a constant defining the symmetry of the curve.

If plant population growth is to be accurately predicted, r, the intrinsic growth rate, and K, the ceiling on individual plant size, must be variable rather than constant. Earlier I suggested that RGR, which for open-grown trees is the r of equation (5), was roughly proportional to the inverse of plant size. Hozumi (1980) used the density-dependent maximum plant size defined by the self-thinning rule as a K value – an especially nice approach because it links plant growth rate directly to stocking density. Aikman and Watkinson (1980) modified the standard logistic approach by assuming that unconstrained growth was a function of the area occupied by a plant rather than of its size, and that growth constraints (the damping term) were produced by competitive constraints on area. Their model provides for differential competitive ability among individuals – one of the few linking growth dynamics to population structure.

Although rarely used in plant population dynamics, a Lotka-Volterra approach (a set of coupled logistic equations) may be used to model competitive interactions between individuals. This was done by Yamamura (1976), and by Vandermeer (1981), who used his model to derive density-dependent conditions for transgressive yields in species mixtures.

One of the nice things about a mechanistic model, such as the logistic, is that it confers analytical power. Take, for example, the basic logistic, equation 5, with r proportional to B^{-1} and K proportional to ρ^{-x} (from the self-thinning rule):

$$\frac{1}{B}\frac{dB}{dt} \propto \frac{1}{B} \quad (1-C_1B^a\rho^{ax}) \tag{6}$$

Multiplying both sides by ρ, the stocking density, gives an expression for relative growth rate of the stand (RGRS):

$$\mathrm{RGRS} \propto \frac{\rho}{B}(1-C_1Ba\rho^{ax}) \tag{7}$$

differentiating equation (7) with respect to ρ, setting the resultant equation equal to zero, and solving ρ in terms of B (an elementary maximization technique of the Calculus) gives:

$$\rho_m = \left(\frac{1}{1+ax}\right)^{1/ax}\left(\frac{C}{B}\right)^{1/x} \tag{8}$$

where ρ_m is the stocking density which maximizes stand growth, given an average plant biomass, B. Note that ρ_m varies with a, the parameter determining symmetry, and x, the absolute value of the self-thinning slope. Though such analytical approaches undoubtedly oversimplify the real world, they generate testable hypotheses and provide a foothold in the mechanics of the competition process.

Although logistic equations are typically used to model the time rate of change in a quantity, they can be used in other ways. Westoby (1982), for example, introduced the notion of 'Distribution Modifying Functions' (DMFs), which relate the growth of a plant to its relative size within the community, rather than to its absolute size. He showed that the form of the DMF influenced the size distribution within a population, with a logistic DMF producing the empirically observed bimodal distribution.

C. Holistic models – thermodynamics and Maxwell's ecological demon

The need for holism (synthesis) as well as analysis is self-evident to most scientists (cf Odum 1977); what have been lacking are the tools. Information theory was received enthusiastically by many biologists as, at long last, a theoretical foothold into pattern, but with some notable exceptions (eg Gatlin 1972) it has produced no new biological insights. This is not because the concept of a holistic approach to understanding pattern is a bad one, but rather because biological patterns are much more subtle and complex than simple communication systems (cf Johnson 1970); neither can information theory tell us much about human language, and for the same reasons.

I believe we are on the threshold of a very exciting time in ecology, one in which the theoretical tools of holism will yield new insights into the properties of systems. For example, Axelrod and Hamilton (1981) recently used game theory to investigate the evolution of co-operation, and Wiley and Brooks

(1982) produced a new theory of evolution based on nonequilibrium thermodynamics. In this section, I will discuss one way in which competitive interactions may be interpreted in the context of General Systems Theory.

Laszlo (1972, p. 43) states the principles of self-organization in the following formula:

$$\begin{matrix}\text{External} \\ \text{forcings}\end{matrix} \rightarrow \begin{matrix}\text{Internal} \\ \text{constraints}\end{matrix} \rightarrow \begin{matrix}\text{Adaptive} \\ \text{self-organization}\end{matrix}$$

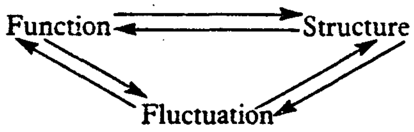
Earlier I discussed competition in systems which include one nitrogen-fixing species, and pointed out that the competitive interaction between the higher plants was mediated by a third species – the nitrogen-fixing symbiont. In the context of Laszlo's scheme, nitrogen is an internal constraint of this system, and the nitrogen-fixing symbiont the 'external forcing' acting on that constraint. The result, 'adaptive self-organization', is a restructuring of the new, three-species system in niche space (along the nitrogen axis), with a concomitant increase in system productivity.

A related view, with perhaps more potential for quantitative analysis, is in terms of nonequilibrium thermodynamics. Prigogine's (1980) equation for entropy production in a nonequilibrium system is:

$$ds = d_e s + d_i s \tag{9}$$

where ds is total entropy production, $d_e s$ is entropy flow across system boundaries, and $d_i s$ is internal entropy production. Schrödinger (1945) pointed out that organisms maintain structure because they 'import negentropy', that is $d_e s$ is negative. Similarly, the entry of *Rhizobium* into a grass-legume system may be viewed as an importation of negentropy which increases internal structure. In effect, the nitrogen fixer acts as a 'Maxwell's Demon'[2], decreasing the randomness (and therefore the entropy) with which the species occupy niche space.

Analogies between ecological systems and the chemical systems of thermodynamics are perhaps more heuristic than literal. Nevertheless, if there are 'general systems properties', such analogies may bear fruit in ecology (Prigogine 1980). For example, stable, nonequilibrium structures ('dissipative' structures) are characterized by three factors in the theory of nonequilibrium thermodynamics: 'the function, as expressed by the chemical equations; the space-time structure, which results from the instabilities; and the fluctuations, which trigger the instabilities. The interplay between these three aspects:



leads to the most unexpected phenomena, including order through fluctuations . . .' (Prigogine 1980, pp. 100–101). If we identify function with productivity, and fluctuation with the flow of negentropy, and generalize space-time structure to niche-space structure, Prigogine's scheme precisely describes the

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[2] James Clerk Maxwell suggested that the second law of thermodynamics could be violated, in principle, if there existed 'an intelligent being small and agile enough' to sort the molecules in a gas into fast and slow, and thus decrease its entropy. Such an imaginary being came to be known as Maxwell's Demon (quote from Campbell 1982, p. 48).

relationships underlying co-evolutionary interaction within ecosystems, including those which we characterize as competitive. Clearly, the entry of new species (or flows of negentropy) into a pre-existing system does not always increase its structural complexity, or result in a new stable equilibrium containing all the elements of the old system (eg ingestion of carcinogens; introduction of gypsy moth, Dutch elm disease, chestnut blight; spraying Agent Orange). Such an event may be as rare as a successful mutation, but like a successful mutation it could result in an evolutionary advantage to the species-systems.

Some system-level concepts, such as Westoby's (1982) distribution modifying functions, Kikuzawa's (1984) 'stand compactness', and the notion of 'competitive tension' which I discussed earlier, may have predictive potential. On the other hand, the primary advantage gained from holistic models may be new ways of viewing systems. The importance of the latter should not be under-estimated, because it is in the context of our paradigms[3] that we formulate questions, design experiments, and interpret results.

IV. ON PARADIGMS AND LANGUAGES

Although the notion of trees as crop plants says nothing more than that trees can be managed to produce value for humans, it is difficult to avoid associating this concept with the techniques of modern agriculture – in which genetic and structural heterogeneity is eliminated, and the consequent loss in system buffering is replaced by high energy inputs. The way we act on the world is determined by how we view the world: in the words of Barrett (1978), 'Technique has no meaning apart from some informing vision'. It is essential to ask from time to time whether our world view is still appropriate; I believe that we are at such a juncture in both agriculture and forestry.

The development of agriculture was a marvellous statement of human ingenuity; however, it was also a product of ignorance, and its emergence as a modern technology was characterized by both brilliant tactics and questionable strategy. Agriculture was a product of ignorance in that its development assumed the patterns of nature to be chaotic, and its techniques flowed from the logical extension of that assumption, that chaotic systems must be dealt with by reduction to understandable, and therefore manageable, subsystems (individuals). The more we learn about ecosystems, however, the more it becomes obvious that they are far from chaotic. They are, in fact, reminiscent of human language in that, just as communication depends on syntax (the arrangement of words with respect to one another) and on context (the historical setting of the words), so ecosystem function cannot be understood outside the syntactical relationships between organisms and the historical context of co-evolution.

The strategy of modern agriculture assumes that (a) the buffering capacity of natural systems, which is based on information (eg genetic and structural diversity), can be adequately replaced by energy inputs, (b) unlimited supplies

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[3] A paradigm is an example or pattern of the inflexion of a part of speech; the term is also used to mean a general pattern or model.

of energy will be available for this buffering, and (c) no major climatic changes will occur. It is still unclear whether the first assumption is correct, but the second depends on the development of new energy sources, and the third is manifestly false.

Foresters must not become too enamoured with the techniques of agriculture at a time when agricultural techniques themselves must be seriously re-evaluated. It is very important, in the face of an uncertain future, to keep our options open. This does not mean that we should not manage forests, but rather that we should intensify our efforts to learn the language of nature, so that we can merge with it and produce not only abundance, but security in an uncertain and rapidly changing global environment.

ACKNOWLEDGMENTS

Research was funded by the Long Term Ecological Research Program of the National Science Foundation, and by the Mapleton Ranger District of the Siuslaw National Forest (USDA Forest Service). I thank the following for data collection, analysis, and helpful discussion: Paul Schroeder, Carloyn Choquette, Mark Miller, Betsy Kaiser, Greg Koerper, Jeff Borchers, Emily Semple, and Kyna Perry. Thanks are also due to Melvin Cannell and David Ford for review and editing, and to Carol Rosenblum Perry for teaching me that language is more than words, and knowledge more than analysis.

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