Chapter (non-refereed)

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BIOLOGICAL OPPORTUNITIES FOR GENETIC IMPROVEMENT IN FOREST PRODUCTIVITY.

By M.G.R. CANNELL

Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland.

SUMMARY

The genetically variable attributes that influence forest productivity can be divided into three groups.

First, there are attributes which can be, and are being, improved, normally as the unplanned consequence of selection for genotypes which produce the largest, highest-quality individuals in the shortest time. These include adaptive traits, enabling trees to more fully exploit available growing seasons, and more effectively deal with or endure adverse features of the environment (especially water stress). These adaptive traits are becoming understood from studies on provenances, and could be used as early selection criteria. Individual tree 'vigour' and, in a sense, gigantism, are being favoured, by selecting for rapid establishment, rapid individual tree crown development, root regeneration and 'site capture', possibly favouring competitive types and enhancing early sawlog production. And, most of all, stem quality defects are being minimized or eliminated.

Secondly, there are attributes which could be improved, but which are not being fully exploited. It is often considered too costly, too risky or potentially counterproductive to attempt to tailor genetically more uniform populations to particular sites or cultural environments. These judgements need to be regularly reviewed. Opportunities for genetic improvement in biomass yields may be particularly large under intensive culture, because of lessened need for mutually-depressing competitive traits, and smaller investment of assimilates in

non-harvested branches and roots. More attention might also be given to selection for delayed ageing, avoiding early flowering genotypes, and employing new technologies to induce parent trees to flower.

Thirdly, there are attributes which do not seem readily amenable to genetic improvement, even though attempts may be made to improve them. Foremost among these attributes may be fundamental changes in the potential radiant energy conversion efficiencies of well-adapted closed forest stands. It is pointed out that (a) in temperate regions, natural, coniferous forest stands are potentially already among the most productive biomass producers of all terrestrial crops, (b) contrary to common belief there are few precedents in agriculture for substantial genetic improvements in yield resulting from selection for greater photosynthetic efficiency of crop stands, including vegetative crops like grasses (Alberda 1971), and (c) it may be particularly difficult to improve the per hectare biomass productivities of forest stands as long as we need to select for rapidly growing competitive individuals, because compromises have to be made between traits desired for rapid site capture and competitiveness, and traits desired for maximum community productivity after full site capture.

RÉSUMÉ

Les attributs variables sur le plan génétique qui influencent la productivité de la forêt peuvent se diviser en trois groupes:

Premièrement, il existe des attributs qui peuvent être, et sont, améliorés; en général, ces améliorations sonts la conséquence, non planifiée, d'une sélection de génotypes qui produisent, dans le temps le plus court des individus les meilleurs en qualité et en dimension. Ces attributs comprennent les facteurs d'adaptation, qui permettent aux arbres d'exploiter au maximum les saisons de végétation et de lutter le plus efficacement possible contre les facteurs adverses de la nature (surtout contre le manque d'eau). La connaissance que l'on a des facteurs d'adaptation provient des études des provenances et peuvent être utilisés comme premiers critères de sélection. La 'vigueur' d'un arbre, et dans un certain sens, le gigantisme, sont favorisés par la sélection pour une reprise rapide, un développement rapide de la cime de l'arbre, une régénération rapide des racines et une exploitation rapide du potential de la station, favorisant eventuellement le pouvoir compétitif et arrivant ainsi rapidement à produire des bois de sciages. Et surtout les défauts de qualité du tronc sont minimisés, ou même éliminés.

Deuxièmement, il y a les attributs qui seraient à même d'être améliorés mais qui n'ont pas encore été complètement exploités. On a souvent pensé qu'essayer de créer des peuplements génétiquement plus uniformes pour des stations ou des milieux particuliers, était un procédé trop côuteux et trop risqué, qui irait même à l'encontre du résultat désiré. On se doit de réviser ce jugement régulièrement. Les possibilités permettant une amélioration génétique du rendement en biomasse peuvent être très importantes dans le cadre d'une culture intensive parce que la compétition entre individus est moins grande et l'investissement en produits de photosynthèse dans les branches et les racines non recoltées est plus faible. On devrait aussi porter plus d'attention à la sélection portant sur un vieillissement retardé et éliminer les génotypes qui fleurissent trop tôt et sur l'utilisation de techniques nouvelles pour induire la floraison chez des arbres-mères.

Troisièmement, il existe des attributs qui ne semblent pas être améliorables, bien que l'on ait essayé. L'attribut le plus important parmi ceux-ci est celui qui amènerait un changement fondamental dans l'efficacité de la conversion potentielle de l'énergie de radiation dans des peuplements fermés et bien adaptés. Il faut remarquer que (a) dans les régions temperées les peuplements naturels de résineux sont déjà parmi les meilleurs producteurs de biomasse de toutes les productions terrestres, (b) contrairement à l'opinion commune, il y a peu de précédents en agriculture qui montrent une amélioration génétique importante du rendement, qui résulterait d'une sélection basée sur une plus grande efficacité de la photosynthèse dans les peuplements, y compris les prairies

(Alberda 1971) et, (c) il serait particulièrement difficile d'améliorer la productivité de biomasse par hectare dans les peuplements forestiers si l'on continue à choisir des essences à croissance rapide et compétitive, car on doit trouver un compromis entre, d'une part, l'utilisation plus rapide du potentiel de la station et une certaine compétition, et d'autre part une productivité maximale de l'ensemble du peuplement après une occupation complète de la station.

ZUSAMMENFASSUNNG

Die genetischen Eigenschaften, welche die Produktivität eines Waldes beeinflussen, lassen sich in drei Gruppen gliedern.

Erstens gibt es Eigenschaften, die sich verbessern lassen und die auch wirklich verbessert werden. Normalerweise geschieht das als ungeplante Folge der Selektion von Genotypen, die in der kürzesten Zeit die grössten und qualitativ besten Einzelexemplare hervorbringen. Zu diesen Eigenschaften gehört auch die Fähigkeit der Anpassung, aufgrund derer die Bäume die Wachstumsperioden intensiver nutzen und widrigen Umweltbedingungen (besonders Wasserknappheit) standhalten können. Diese Merkmale der Anpassungsfähigkeit werden aus Provenienzstudien klar ersichtlich und könnten als erste Selektionskriterien dienen. In der Selektion auf raschen Bestandesschluss, rasche individuelle Entwicklung der Baumkronen, Regenerationsfähigkeit der Wurzeln und 'Eroberung des Standorts' hin werden die Wuchskraft von Baumindividuen und in gewissem Sinn auch Riesenwuchs bevorzugt. Man versucht nach Möglichkeit, wettbewerbsaktive Typen besonders zu fördern und damit eine frühe Sägeholzproduktion zu steigern. Vor allem aber werden Qualitätsmängel bei den Baumstämmen auf ein Minimum reduziert oder sogar ganz verhindert.

An zweiter Stelle stehen Eigenschaften, die zwar verbesserungsfähig sind, aber nicht voll genutzt werden. Es gilt häufig als zu kostspielig, zu riskant oder der Produktivität möglicherweise abträglich, wenn man versucht, genetisch gleichformigere Populationen für bestimmte Standorte oder Umweltbedingungen zu schaffen. Solche Ansichten sollten in regelmässigen Abständen neu überdacht werden. Bei intensiver Bewirtschaftung gibt es besonders viele Möglichkeiten genetischer Verbesserung der Biomasseerträge, da weniger Bedarf besteht für gegenseitig unterdrückende und rivalisierende Eigenschaften und somit weniger Assimilate den nicht genutzten Zweigen und Wurzeln zugeführt werden. Man könnte auch der Selektion im Hinblick auf eine Verzögerung des Alterns mehr Aufmerksamkeit schenken, indem man frühblühende Genotypen vermeidet und neue Methoden anwendet, um die Mutterbäume zum Blühen zu bringen.

Drittens gibt es Eigenschaften, die nicht ohne weiteres genetisch zu verbessern zu sein scheinen. Dennoch könnten entsprechende Versuche unternommen werden. Grundsätzliche Veränderungen in der potentiellen Fähigkeit von gut angepassten, geschlossenen Waldbeständen, den Ausnutzungsgrad der Strahlungsenergie zu steigern, können an erster Stelle in der Reihe dieser Eigenschaften stehen.

Es wird darauf hingewiesen, dass (a) in gemässigten Zonen natürliche Nadelwaldbestände heute schon potentiell zu den produktivsten Erzeugern von Biomasse unter allen Landpflanzen gehören; (b) im Gegensatz zur allgemeinen Auffassung es in der Landwirtschaft nur wenige Beispiele für substantielle genetische Verbesserungen des Ertrags gibt, die durch die Selektion im Hinblick auf grössere photosynthetische Effizienz von Pflanzenbeständen, einschliesslich vegetativ vermehrter Pflanzen, wie Gräser (Alberda 1971), erzielt wurden; und (c) es sich als besonders schwierig erweisen kann, den Biomasseertrag der Waldbestände pro Hektar zu verbessern, so lange wir nach rasch wachsenden resistenten Einzelpflanzen selektieren müssen, weil Kompromisse nötig sind zwischen Merkmalen, die wegen rascher Standortseroberung und Resistenz erwünscht sind und Merkmalen, die wegen ihrer optimalen allgemeinen Produktivität nach der vollen Eroberung des Standorts wünschenswert sind.

INTRODUCTION

The yields of modern varieties of most field and horticultural crops are several-fold those of their wild progenitors, partly as a result of selection and breeding. Could the growth rates and yields of forest plantations be increased similarly by breeding, bearing in mind that forest trees are only at the threshold of domestication? What are the biological constraints and limits on forest productivity set by their physiology and the way they are grown?

This contribution gives some personal viewpoints on these questions based on considerations of (a) the physiological basis of yield of forest trees - their strengths and weaknesses as productive systems, and (b) the yield-determining processes that have been improved by selection and breeding in field crops (Wallace, Ozburn & Munger 1972; Ivins 1973; Evans 1975).

To provide a framework I shall examine four broad categories of attributes which have to be improved in order to increase forest productivities - attributes affecting

(a) adaptation,
(b) the speed of 'site capture' to full canopy cover after planting and each thinning,
(c) the efficiency of 'site utilization' in terms of dry matter productivity per hectare per year after full site capture, and
(d) the proportion and value of the dry matter that is harvested.

ADAPTATION

The biological potential for improving forest yields by selecting species and provenances which are better adapted for volume growth than local populations is well-known. Many locally native forest populations, like primitive cereals and maize (Evans & Dunstone 1970; Mangelsdorf, MacNeish & Galinat 1964) seem to exploit environmental resources rather conservatively, sacrificing rapid growth for long-term stress tolerance, ensuring survival over an evolutionary time scale, always in the face of competition from other species. Similarly, native provenances of trees often appear to under-utilize the growing season available to them in their localities, or they may seem to be 'over-sensitive' to mild levels of water stress. These may have been desirable strategies during their evolutionary history, but during the 20-30 years history of provenance research they have seemed over-cautious. There is a prodigious literature on the benefits of provenance transfer from long-season, wet or otherwise favourable climates, to shorter-season, less-favourable climates (e.g. Wright 1976; Farmer 1976). The fastest growing provenances are often from areas with somewhat longer seasonal periods of shoot, bud or cambial growth or, in the case of Pinus taeda, for instance, are from areas with more frequent or reliable summer rainfall (Wells 1969).

But all individuals within a forest population are not equally well-adapted. Progenies selected within provenances differ in their abilities to endure or exploit particular environmental conditions. Kleinschmit & Sauer (1976) found more variation in shoot growth phenology among clones within provenances of *Picea abies* than between provenances, and van Buijtenen, Bilan & Zimmerman (1976) found considerable variation in drought resistance among families belonging to certain provenances of *Pinus taeda*. Thus, during the early generations of recurrent selection, there is considerable scope to improve the adaptive traits of the best provenances. This selection could be done most effectively, and perhaps at an early age, if we gained and used information on the physiological and morphological basis of provenance differences.

Provenance differences in phenology can be traced to particular temperature and photoperiodic thresholds for budburst budset and bud development (e.g. Campbell 1974; Ekberg et al. 1976). Desirable genotypes may have enhanced temperature or photoperiodic sensitivities at particular thresholds or may be indifferent to photoperiod. In fact, the shoot apices of *Picea* spp. may already be indifferent to photoperiod during bud development (Pollard & Logan 1977), in which case temperature thresholds for growth and frost hardiness may be all important. It is noteworthy that the photoperiodic requirements of maize, soybean, potato and some rice varieties have been relaxed during selection to enable them to utilize the full growing seasons at temperate latitudes. In these, and many other annual field crops, temperature thresholds for vegetative growth seems to limit yields (Monteith & Elston 1971).

Provenance differences in crown form can be traced to a few rules governing the branching patterns (Cannell 1974; Cochrane & Ford 1978). Differences in drought resistance can be traced to particular avoidance or tolerance mechanisms, and so on.

The biological potentials for forest productivity are set not only by how well the trees are adapted to particular natural environments, but also how well they are adapted to the management system nder which they will be grown. Most tree breeders select genotypes which will grow well in a range of climates, at various nutrient levels and with current site preparation and forest management. This may be wise, but the history of agriculture suggests that we could be missing large and perhaps profitable opportunities for genetic improvement if we do not explore the potential genetic gains under intensive culture, ignoring, for the moment, the high costs of support energy. The outstanding feature of many field crop improvement programmes has been the synergism between new varieties, fertilizers, weed control and an increase in planting density. The prime achievements of cereal breeding have been adaptations to fertilizers and close spacing. Without them, genetic improvement by selection would probably have been small. Indeed, Zohary (1969) reported that the grain yield from mixed stands of the wild progenitors of wheat, barley and oats in the Middle East were similar to the yields of wheat in England, and rice in Japan, during the Middle Ages, that is, before the age of artificial fertilizers. A few researchers who are examining biomass and pulp production by trees with intensive culture, report very high yield of particular genotypes using high rates of fertilizers and close spacing (Schultz 1975; Anon 1976).

Unfortunately, the information on exploitable interactions between tree genotypes and their cultural environments is scanty. Researchers are only just beginning to explore the responses of large single-family blocks to various management regimes (Bridgwater & Stonecypher 1978). There is, however, evidence that phosphate-responsive varieties of Pinus taeda and Pinus elliottii could be developed for phosphate - deficient sites, and certain specific crosses within these species are exceptionally responsive to nitrogen fertilizers (Goddard, Zobel & Hollis 1976). Campbell & Wilson (1973) found no full-sib x spacing interactions among young Pseudotsuga menziesii, but Snyder & Allen (1971) and Adams, Roberds & Zobel (1973) found evidence that competitive ability had a genetic component in Pinus elliottii and Pinus taeda, respectively.

An important trait which could be regarded as adaptive, is the length of the life cycle. Different species, families and even clones mature at different ages, which partly determines the shapes of their height : age progress curves and times of maximum current annual increment (Muckadell 1959; Wareing & Matthews 1973). The onset of these genetically determined ageing processes (inheritance studied in fruit trees, e.g. Visser 1976) is usually signalled by increased cone production and a loss of apical dominance. Some species (e.g. Pinus virginiana) and some provenances (e.g. Lulu Island, B.C. Pinus contorta growing in Britain) are undesirable because of early ageing. Less obvious family differences in ageing may not become apparent for many years, and should, where possible, be observed on their parents. There could be dangers in selecting heavily flowering plus trees, particularly if they are not very old.

How far it is wise to go in fine-tuning the adaptive traits of forest trees, is a matter of judgement. Improvements in the fitness of varieties to particular natural or man-modified environments carry with them deteriorations in their abilities to cope with spatial and temporal variations: adaptation and adaptability are antagonistic (Simmonds 1962; Tigerstedt 1974). Most tree breeders prefer to breed for widely adapted types which are genetically heterogeneous and physiologically adaptable. These types will perform as expected in a wide range of niches and environments and will exercise least selection pressure on potential pests and pathogens. Risks and breeding costs will be modest, but there will inevitably be sacrifices in potential genetic gains as long as some genotypes remain poorly adapted. The traditional approach of foresters is, in many respects, like that of subsistence farmers: aimed at some yield in most years on most sites, and satisfied with a modest overall optimum yield rather than striving for the maximum possible. A modest step towards adaptive fine-tuning, involving little further breeding costs, would be to assign single families to uniform sites and cultural treatments to which they respond (Bridgwater & Stonecypher 1978). Further steps would be to grow single blocks of full-sib families or clone mixtures. These steps should not be rejected for reasonably uniform sites, bearing in mind that even single clones can be phenotypically plastic (Bradshaw 1965). Thus, some tree genotypes can acclimatize more readily than others to changes in temperature and light intensity (Ledig 1976; Ledig, Clark & Drew 1977). A few potato clones are highly adaptable, and growers of tea and rubber have managed extensive areas with genetically homogeneous perennial crops for many years. We should also be aware, however, that many studies have shown that cereal cultivar mixtures slightly outyield completely pure stands (Simmonds 1962) and that coffee (an inbreeding species), which is genetically homogeneous, was wiped out of Sri Lanka by leaf rust.

SITE CAPTURE

A coniferous forest crop may spend half the total rotation 'capturing' and 'recapturing' the site, that is, exploring the soil profile and building up a full foliage canopy after planting and after each thinning. Consequently, forests, like annual crops, probably assimilate carbon and accumulate dry matter at rates which are proportional to the amount of intercepted radiation over the life of the crop (Monteith 1977). It is important, therefore, to increase the speed of 'site capture'. On fertile, lowland sites hardwoods will restore their foliage canopies rapidly, and if they are coppiced their soil environments are explored almost continuously. With conifers, however, we must endure the prolonged period of early crown development of new saplings, and accept that the soil profile has to be re-explored with new roots when a tree is felled.

It is important to realize that the biological attributes which limit the speed of site capture are those which limit the growth rates of trees as individuals. Many of these attributes are different from those influencing the per hectare productivity of closed forest stands (Cannell 1978).

It is equally important to realize that almost all forest tree breeders evaluate the growth of genotypes on the basis of the mean sizes of individuals, normally in rows, before or after canopy closure. They do not, and cannot, evaluate families on a per hectare basis in blocks large enough to allow the spatial processes of competition to operate (Ford 1975), because of the cost and the environmental heterogeneity of forest sites. Because they select for rapid individual tree growth, tree breeders are successfully improving many attributes favouring rapid site capture, involving rapid exploration of surrounding environmental resources, and increased competitive ability. These improvements will be inevitable consequences of selecting for fast-growing individuals, and will be highly desirable for half the rotation. During the other half, when the sites are fully captured, intensified inter-tree competition could have two effects. On the negative side, it could conceivably depress per hectare productivity (Fig. 1). This is because, to maximize volume production per hectare, a large proportion of the trees should produce large volumes per year by using environmental resources efficiently, and not by robbing them from their neighbours (Donald 1968; Ford 1976; Cannell 1978). On the positive side, intensified inter-tree competition may spread tree size frequency distributions (producing some large dominants) and so enhance the chances of producing some large trees of high value early in the rotation (Fig. 1). According to Schwanitz (1966) one of the important steps in the evolution of crop plants has been a transition to gigantism, often involving hybridization or an increase in ploidy. Large cereal grains, maize cobs, beans and beets, like large trees, are more valuable than small ones. Selection for gigantism in trees may be a worthwhile pursuit in itself, irrespective of its possible negative effect on per hectare volume productivity.

What are the biological attributes which regulate the speed of site capture? First, they will include the size of the embryonic capital and other factors which influence seedling size in the nursery and after outplanting (e.g. Sweet & Wareing 1966; Perry 1976). The value of W in the equation $W=W_0^{rt}$ depends on the starting value W_0 as well as the relative growth rate, r, and time, t. So-called 'superseedlings' of *Pinus taeda*, *P. elliottii* and *P. echinata*, selected in the nursery, can be 20-200 per cent greater in individual-tree volume at age ten than trees gorwn from average-sized seedlings (Zarger 1965), and differences in the initial size of *Pinus radiata* cuttings can lead to 4-5-fold overestimates of genetic gain at age four (Burdon & Sweet 1976). Maternal, seed size, nursery and 'C' effects could be exploited to speed the rate of site capture.

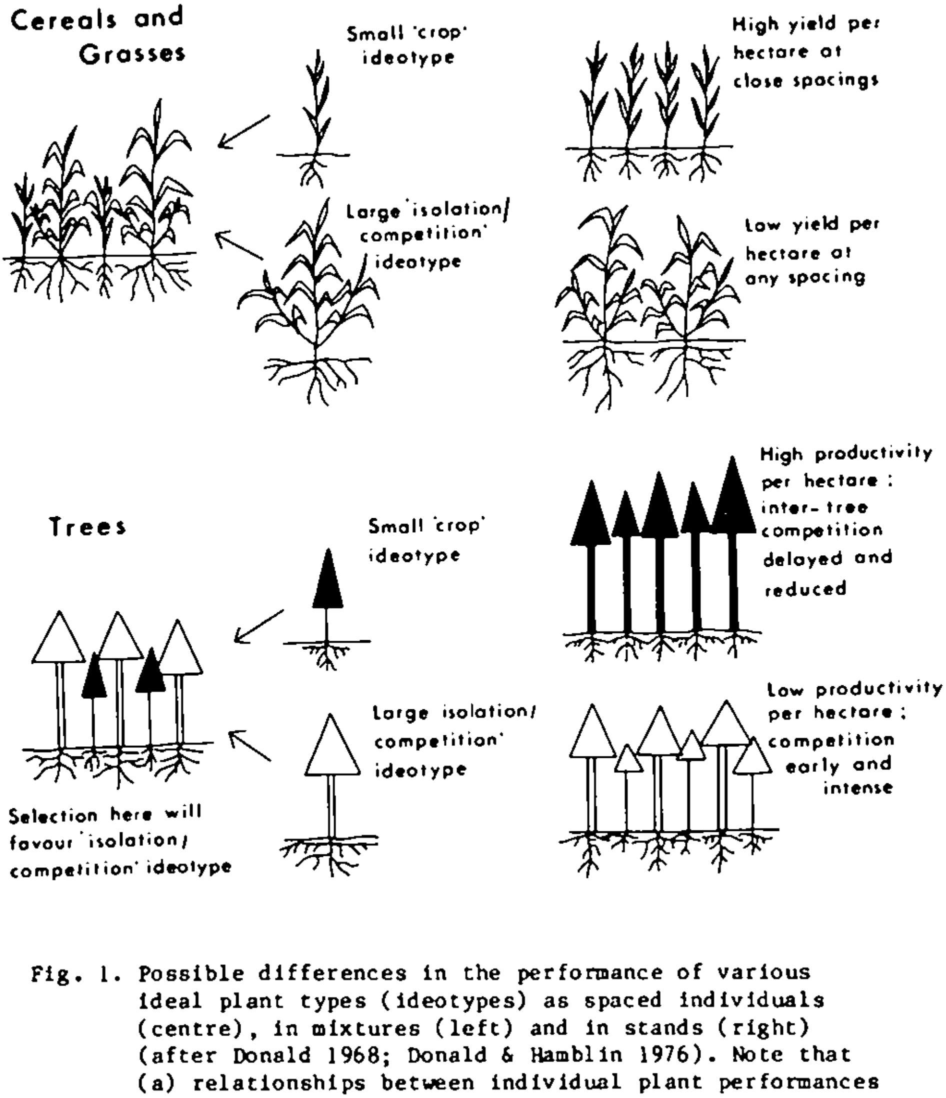

Fig. 1. Possible differences in the performance of various ideal plant types (ideotypes) as spaced individuals (centre), in mixtures (left) and in stands (right) (after Donald 1968; Donald & Hamblin 1976). Note that (a) relationships between individual plant performances and per hectare productivity after canopy closure can be negative (Hamblin & Powell 1975), (b) 'isolation/ competition' ideotypes may tend to be selected if the criterion is plant size, and (c) selection for 'isolation/competition' ideotypes may lead to a desirable early spread in tree size frequency distributions.

Secondly, among the factors influencing r in the above equation, is the rate of leaf area expansion. In general, plants which invest a large proportion of their dry matter in photosynthetic tissue and distribute that tissue over a large surface area (often producing 'thin' leaves) to increase light interception, tend to succeed as individuals (Jackson 1963; Potter & Jones 1977). Relative leaf growth rates are important determinants of the time taken to develop fully light-intercepting crop canopies. Within conifer species there are striking differences in branching and crown form which influence the rate of build-up in photosynthetic tissue after planting and thinning. The components have been considered (Campbell 1963; Miller 1965; Cannell 1974) and are contained in crown expansion factors in single-tree computer models (Arney 1972; Mitchell 1975). Unfortunately, we cannot select rigorously for rapid crown development because of its undesirable impacts on stem knot size, wind stability and resistance to snow breakage. Very coarsely-branched, wide-crowned trees are rejected in favour of trees with moderately full crowns of fine branches, recognizing that there is a strong relationship between bole size and crown size (e.g. Waring et al. 1977). Also, genotypes which display current-year needles as late summer flushes may be superior on favourable sites to genotypes which store all their needle primordia in buds until the following year.

Thirdly, inherent differences in root morpholoy and mycorrhizal development may be important. In droughty or competitive situations early growth after transplanting may be limited by the speed of access to water and nutrients, rather than the speed of radiant energy capture. In these situations, breeders, selecting fast-growing progenies, may be selecting for increased root growth (e.g. Pinus taeda, Cannell, Bridgwater & Greenwood 1978). If so, this seems somewhat wasteful because trees, like land races of field crops (Jennings 1976) may already invest heavily in roots as a survival strategy in competitive habitats. Young conifers send up to 50 per cent of their fixed carbon below ground (Webb 1977). It would be better if some of this dry matter were employed in shoot growth, but apparently this is not possible as long as there is a need for rapid root regeneration after transplanting. It would be interesting to know whether known genetic differences in root : shoot relative growth rates (Ledig & Perry 1965) could bring about interactions between genotypes and planting techniques or environments. If so, this would be another instance where genetic improvements were conditional upon improvements in tree culture.

So far, I have spoken of attributes which influence light, nutrient and water 'capture'. To these must be added attributes which improve the efficiency with which light is intercepted, carbon fixed and water and nutrients used, remembering that we are considering these traits for individuals and not for forest stands. The ideal light interception characteristics of isolated plant canopies (Charles-Edwards & Thornley 1963) are different from those of crop canopies (Duncan et al. 1967). High rates of light-saturated photosynthesis which are desirable for isolated plants may be less important in crop stands because most leaves are then shaded. And we should be aware that light-saturated photosynthetic rates, or net assimilation rates, have not been improved much during the evolution of many field crops (Evans 1976 and see below), possibly because high photosynthetic rates are associated with small mesophyll cells, small leaves and slow leaf relative growth rates which mean slow rates of 'site capture' (Charles-Edwards 1978).

Nevertheless, potential genetic improvements in the growth rates of individual trees, resulting from improvements in rates of site capture combined with better adaptation, appear to be considerable. Widely spaced trees of some new poplar clones grow twice as rapidly as old ones (van Goor & Koster 1969). And many conifer breeders confidently predict 50 per cent genetic gains over 2-4 generations of recurrent selection for individual-tree heights and bole volumes, attainable without intensive culture or intensive exploitation of genotypes x environment interactions. However, such figures for gains in yield may apply in full, as gains per hectare, only during the periods of site capture, and they are, of course, modest compared with the several-fold genetic gains in, for instance, wheat and rubber yields since their domestication (rubber: Ferwerda 1969).

SITE UTILIZATION

Once the site has been fully captured the productivity of a forest depends on how effectively finite resources of light, water and nutrients are utilized by the community. As mentioned above, whilst it is desirable to have some vigorous, competitive individuals to rapidly produce some large high-value stems, intense competition throughout even-aged stands could well depress per hectare productivity of dry matter and wood volume (Fig.1). The need to compromise between vigorous, competitive, pioneer-like individuals, and those which contribute to high per hectare productivities after full site capture, could severely limit potential genetic gains in per hectare volume production averaged over complete rotations.

This dilemma becomes clearer when we consider the traits that need to be compromised. First, there is the compromise between reasonably wide, spreading crowns giving rapid site capture and tall, narrow crowns which apparently intercept light most effectively in closed canopies (Jahnke & Lawrence 1965) and produce the greatest stem volume per unit of crown volume or surface area (Assman 1970; Hamilton 1969). Secondly, there is the compromise between characteristics giving maximum photosynthetic rates at light-saturation, desirable on open-grown trees, and maximum shade adaptation, light absorptivity and photochemical efficiency, more important for shaded needles in conifer stands with leaf area indices often greater than ten (see Cannell 1978). Thirdly, there could be compromises between below-ground nutrient-capture and drought-avoidance mechanisms desirable for open-grown individuals, and adaptive traits needed to utilize, mobilize and recycle nutrients effectively, and contend with water stress, in forest stands. In general, the compromises are between traits ideally expressed by what Donald & Hamblin (1976) called 'isolation/competition' ideotypes and 'crop' ideotypes. The 'isolation/competition' ideotype for cereals is a lax, free-tillering, leafy plant, able to explore its environment as extensively as possible, whereas the 'crop' cereal ideotype is small, with few, erect leaves, minimum leaf display and few tillers (Fig. 1). In conifers the differences between ideotypes may be more subtle, but the effect on genetic advance may be the same. That is, selection for fast-growing individuals may not increase stand productivity during the years when the site is fully captured. Selection for yield on the basis of spaced plant performance is believed by some agricultural crop breeders to be an ineffective way of increasing yields (e.g. grasses, Lazenby & Rogers 1960-65; cereals, Syme 1972; Fischer & Kertesz 1976; beans, Hamblin & Evans 1976). Similarly, selection of high-yielding competitive individuals in mixed-genotype stands can favour genotypes which perform poorly in pure stands (Fig. 1; Hamblin & Rowell 1975).

However, we should not be complacent about genetically improving the potential per hectare dry matter productivities of closed forest stands. Plantations of well-adapted, but genetically unimproved temperate-zone forests, especially conifers, which are well-supplied with nutrients and water, are already physiologically capable of producing as much dry matter as any highly-bred annual or perennial field crop employing C3 photosynthesis at the same latitude (Fig. 2). In north-temperate regions this is 30-40 Mt/ha/yr or above-ground dry matter - equal to C4 crops in these regions. In certain sub-tropical regions the maximum for forests may be nearer 50 Mt/ha/yr - less than C4 tropical grasses (Dawkins 1963; Bevege 1976; Fig. 2). Reviews by Westlake (1963), Art & Marks (1971), Loomis & Gerakis (1975), Gordon (1975), Kira (1975), and computer models of de Wit (1968) and Monteith (1977), all lead to the conclusion that unimproved coniferous forest canopies are very effective solar energy converters (Cannell 1978). An optimistic interpretation of these figures would be that the potential productivity of genetically improved coniferous

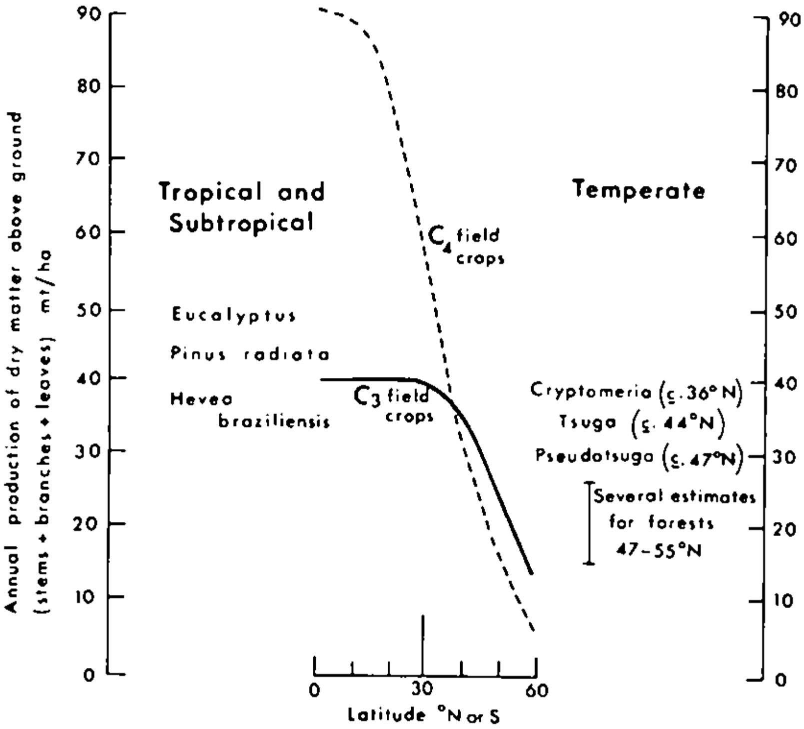

Fig. 2. Maximum annual total above-ground dry matter production recorded for field crops (including perennials) with C3 and C4 photosynthesis (after Loomis & Gerakis 1975), compared with maximum recorded for forest plantations (estimated or taken from Dawkins 1964; Templeton 1968; Westlake 1963; Kira 1975; Cannell 1978). Maximum productivities of temperate hardwoods are less than those of conifers (Day & Monk 1977).

forests may be much greater than that of other C3 crops because of their high capacities for winter photosynthesis (Fry & Phillips 1977), their high leaf area indices (e.g. Grier & Running 1977), high energy conversion efficiencies of shaded foliage, and large cambial sink capacities. On the other hand, attempts to genetically improve the photosynthetic efficiency of field crops in a fundamental sense have been singularly unrewarding (Evans 1975). Computer models constructed by Monteith (1977) and Charles-Edwards (1978) for field crop stands indicate that it would need about a 4- to 5-fold increase in light-saturated photosynthetic rates to bring about a 50 per cent increase in annual dry matter productivity. Genetic variation in photosynthetic rates per unit leaf area within crop species has rarely been positively correlated with productivity, and these rates, or relative growth and/or net assimilation rates, have been negatively correlated with yields among evolutionary races or among modern varieties of wheat (Evans & Dunstone 1970), maize (Duncan & Hesketh 1968), sorghum (Downes 1971), sugar beet (Watson & Witts 1959), sugar cane (Bull 1971), ryegrass (Rhodes 1972), tomatoes and cotton (Evans 1975). The maximum crop growth rates, and radiant energy conversion efficiencies, are remarkably similar for a wide range of C3 crops in Britain and the Netherlands (Greenwood et al. 1977; Sibma 1968; Monteith 1977). It may be very difficult to achieve, say, a 50 per cent improvement in the potential dry matter productivity of well-adapted forest stands in the present-day CO_2 environment by selection within the natural pool of variation in C3 photosynthesis.

I specify the present-day CO_2 environment because global atmospheric CO_2 concentrations are increasing by about 1 vpm/yr, which, according to Monteith (1977) could produce an 11 per cent increase in crop growth rates by the end of the century, without any credit to forest researchers! I also specify the natural pool of variation. According to Charles-Edwards (1978) there is no compelling evidence that crop growth rates can be increased in Britain by selection within the existing genetic variation in leaf photosynthetic characteristics. On the other hand, there could be fundamental biochemical weaknesses universally limiting energy conversion by C3 photosynthesis and existing mitochondrial respiration, which could conceivably be overcome by genetic or chemical modification (Oliver & Zelitch 1977; Day 1977; Radner & Kok 1977). Lastly, I specify C3 photosynthesis becausese all forest trees examined so far are C3 plants (except mangrove, Schaedle 1975; and possibly larch, Fry & Phillips 1976), and in tropical regions potential productivities are greatest with C4 photosynthesis. Crops with C4 photosynthesis can make se of high irradicances, at high temperatures (PEP carboxylase has a temperature optimum exceeding 30°C) and have high water use efficiencies. In temperate regions, however, C4 photosynthesis is at a premium only in summer (Monteith 1978). Over the whole year, especially for crops with high leaf area indices and substantial winter photosynthesis, C3 crops are often more productive than C4 crops (Loomis & Gerakis 1975; Gifford 1974; Moore 1974).

Let me make clear that most closed forest plantations are not producing to the limits of their photosynthetic potential (perhaps 30-40 Mt/ha/yr of above-ground dry matter, about 2.5 per cent solar energy conversion, in north-temperate regions) and selection and hybridization can produce better-adapted genotypes which are more likely to approach this potential especially with inputs of support energy. My point is that we should not be complacement about the prospects of genetically improving this potential energy conversion efficiency of forest stands, particularly if we need to select for big trees.

PROPORTION AND VALUE OF THE DRY MATTER THAT IS HARVESTED.

Diversion of assimilates to the harvested sink (grain, tuber etc.) has been a highly significant feature in field crop improvement. Evans (1976) stated that "the evolution of crop plants has been primarily the evolution of the sink organs". Donald & Hamblin (1976) concluded that "most of the progress in breeding high-yielding cereal cultivars seems to be related to higher harvest indices (HI, the proportion of the aboveground dry matter that is harvested) with little change in biological yield (total dry matter produced)". In the early 1900's the HI of wheat varieties was 32 per cent, whereas for current dwarf wheats it is 49 per cent (Wallace, Ozburn & Munger 1972), Phaseolus bean varieties have HI's ranging from 55 to 67 per cent (Wallace, Ozburn & Munger 1972), potatoes from less than 50 per cent for wild progenitors to 84 per cent for modern varieties (Watson 1971), and rubber clones from 3 per cent to 11 per cent (Templeton 1968), and oil palm progenies from 25 per cent to 55 per cent (Corley, Hardon & Tan 1971). Thus, by changing the HI alone it has been possible to increase crop yields by between 20 and 250 per cent!

Ovington's (1957) study of Pinus sylvestris in England showed that about 40 per cent of the net total dry matter (including needles) produced above-ground by a forest crop is accumulated in the boles and somewhat less than 40 per cent will be recovered and converted into marketable products. If this index could be increased to 50 per cent, this could represent a 25 per cent increase in yield without any increase in total biomass production.

There are certainly considerable genetic differences in dry matter distribution within tree species - in root-shoot allometry (Ledig & Perry 1965; Cannell, Bridgwater & Greenwood

1978) in stem-branch, and bole-crown ratios (Matthews et al. 1975; Thompson 1974) - large enough to increase the above-ground harvest index of indivual trees to maybe 50-60 per cent. However, this potential cannot be fully exploited to increase forest yields as long as these depend greatly on the speed of site capture. As mentioned above, with current forestry practice, it is important to maintain, even enhance, the capacity for rapid crown and root development after transplanting and thinning. Consequently, there is unlikely to be much improvement in bole yields over entire rotations resulting from decreased investment in other tree parts.

One could, however, envisage carefully-planted, regularly thinned, closely-planted plantations, where there was a lesser need for rapid crown development, with inputs of fossil fuels permitting reduced investment in roots and reserves. Under these circumstances, genetic selection for higher harvest indices could increase stem pulpwood yields very considerably, both directly, and maybe indirectly, because the boles require less respiratory maintenance than do additional roots, branches and leaves. It is noteworthy that stem wood production per unit of foliage increases anyway after canopy closure (Mitchell 1975, his p.9 and Fig. 7), either because the trees become photosynthetically more efficient and/or because an increased proportion of the annual dry matter increment goes to the boles (Cannell 1978).

An obvious way to increase the harvest indices of forests is to include the branches, stumps and even structural roots in the harvest (Young 1973; Eskilsson 1974) or improve the technology of harvesting and utilization (e.g. King & Smith 1974). These approaches need not be discussed here.

Fielding (1960) stressed that up to 16 per cent of the above-ground dry matter produced by 7-year-old Pinus radiata can be used to produce strobili, seeds and pollen, and other workers have recorded decreased stem girth increment in heavy-coning years Rohmeder 1951). However, provided there is some effort to avoid very precocious or fecund genotypes (Gerhold 1966), it would be misleading to exaggerate the potential for genetic gain in stem yields by selecting for reduced use of assimilates in flowering and opposed to selection for delayed ageing. If 15 per cent of the annual dry matter increment were taken by cones over one third of the rotation, this would average out as a reduction in vegetative growth of only 5 per cent, even if we assume that the cones are non-photosynthetic and have the same respiratory losses per unit weight as new vegetative tissues. But we know that green fruits, cereal ears, cotton bolls and sexual structures on other plants fix considerable amounts of external and respiratory CO_2 , and that the presence of fruit sinks often enhances photosynthetic rates. In my view, in trees, the association between flowering and ageing is likely to be more important in breeding programmes than the direct impact of flowering on the harvest index.

By far the most important gains in harvest index resulting from current tree improvement programmes will be gains in the proportion of stem wood which has a high merchantable value. Gladstone (1975) and Matthews (1975) elaborated the dramatic gains to be made by diminishing crook, sweep, taper, knot sizes, spiral grain and other quality defects. There may not be much room for altering the proportion of stem to bark, at least in P. taeda (Matziris & Zobel 1973), but most other wood quality characteristics are genetically variable and usually highly heritable. First-generation seed-orchard progenies should contain a much smaller proportion of defective genotypes than unimproved stock. Selection for plant form in field crops (e.g. in brassicas) and elimination of defects (e.g. shattering cereal inflorescences) has been very successful during their domestication (Evans 1976) and will undoubtedly be one of the success stories of forest tree breeding, particularly with pines.

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