THE UPPER LIMIT OF SEEDLING GROWTH 1/

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Abstract.--The absolute upper limit of growth is a
vague and elusive concept. Nonetheless, it is possible to
modify environmental conditions so as to achieve seedling
growth rates far beyond those presently accepted as
standard. Several environmental factors, considered most
important to growth acceleration, are discussed in terms
of their effects on rates of photosynthesis and ontogenetic
development. Although the procedures for manipulating the
environment are experimental and not directly applicable to
mass production, the knowledge derived from such studies
may provide insight into methods for improving the growth
of containerized nursery stock.

INTRODUCTION

The question has often been asked, "What
might be the upper limit of growth for tree
seedlings if all growth conditions were opti-
mum?" In absolute terms, the upper limit of
growth must be thought of as a theoretical
concept. It is a very elusive concept, one
that we cannot as yet define because we are
not familiar with all the ingredients that
contribute to it. The upper limit of growth
involves not only all possible factors of
the environment, but also the complex inter-
actions of these factors with each other and
with the genetic constitution of the seedling.
In other words, to achieve the upper limit of
growth the genetic constitution of the seed-
ling must be pushed to its upper limit, and
it is here that our knowledge is either weak
or lacking.

In spite of uncertainties regarding the
absolute upper limit of growth, we can still
speak in terms of a "potential limit to growth",
or of "maximizing growth." I will use these
terms interchangeably to refer to growth rates
attained when environmental conditions have

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been optimized to the best of our present
ability. Even though these growth rates may
fall short of the absolute upper limit, they
may be "approaching" or "approximating" this
limit. Research to date has demonstrated that
seedling growth rates can be increased far be-
yond those previously accepted as standard by
nurserymen. Such growth rates have been
achieved (1) because of our increased knowledge
of plant response to modified environments, a
 (2) because improved technology has allowed u
to extend the ranges of, and to limit varia-
bilities within, manipulated environments.

In this paper I will begin with a dis-
cussion of the factors that limit seedling
growth, both those inherent within the seed-
ling and those under partial control of the
researcher or the nurseryman. It is only when
these limitations are fully understood that
meaningful methods to overcome them can be de-
vised and the full growth potential realized.
A seedling will attain its full growth poten-
tial when each environmental factor has been
brought to its optimum level. Consequently,
I will discuss in detail several of the more
important environmental factors that can be
readily manipulated. At no time will I spec-
ifically recommend how the growth potential
might be achieved, although I will occasion-
ally refer to the possibilities of accelerating
or maximizing growth in rigidly controlled
environments.

DEFINING THE FACTORS THAT LIMIT GROWTH

Limitations Imposed by Basic Assumptions

Consideration of any theoretical question requires certain basic assumptions to confine it within a manageable conceptual framework. Therefore, in my discussion I will assume a single, uninterrupted growth period from seed germination to, or just prior to, outplanting; that is, I will avoid further complicating the discussion with a dormancy period. Although such an assumption may be justified by its simplicity, certain species might benefit in terms of maximum growth by an intervening dormancy period. In general, the discussion will apply to both hardwoods and softwoods and will be confined to commercial tree species of the north temperate zone.

I will also assume that the genotype has been previously selected for the final re-forestation objective. Consequently, I will not discuss the possibilities of further increasing seedling growth potential either by genetic selection or by breeding for specific juvenile traits. By the same reasoning, I will avoid discussions of seed size, contributions of the endosperm, and other embryo-related growth attributes.

Finally, I will assume no economic con-traints. A preliminary analysis of the the-oretical upper limits of growth should not be constrained by practical questions such as costs of production or seasonal time factors. Major concern throughout this paper will be on producing a vigorous, healthy seedling in the shortest possible time. It must be recognized that such rapidly grown seedlings may not be ideally suited for out-planting. However, once we know how to maximize growth, then we can learn how to modify these condi-tions so as to mass-produce hardy, well-balanced seedlings that can better survive the shock of out-planting to less favorable field conditions.

Limitations Imposed on Utilization of Light

Specific guidelines for a discussion of the upper limit of seedling growth are lacking. Considering the limitations imposed by the foregoing basic assumptions, a logical start-ing point might therefore be the photosynthetic potential of the seedling between the post-germination and the out-planting stages. Photosynthesis is the energy-capturing process and, because we have ruled out the prospects for further improvement of the genome, this process will ultimately determine the upper limit of growth when all other factors have been optimized (Warren Wilson 1969). For this dis-cussion, it is convenient to consider two aspects of the photosynthetic potential: the photosynthetic process and the photosynthetic system.

The Photosynthetic Process

By photosynthetic process I mean the pro-cess by which light energy is captured by the chloroplasts and converted into stored chemical energy for eventual metabolic reactions. Bonner (1962) has shown that the quantum pro-cess of photosynthesis, in which about 10 quanta of light are necessary for the reduction of one molecule of CO_2, has a theoretical effi-ciency of approximately 20%. This is a theo-retical upper limit. The practical upper limit for crop plants grown under non-limiting field conditions, however, is about 5% of the photo-synthetically active radiation, and under average field conditions it is only 2% to 3% (Bonner 1962; Loomis and Williams 1963).

Limitations imposed by the photosynthetic process are largely inherent within the seedling. They involve both biochemical and biophysical reactions that reside within the chloroplast and functional processes related to chloroplast array. By expanding the definition of photo-synthetic process, we might add a list of other mechanisms that are rate-limiting, such as the hinderance of CO_2 movement due to stomatal resistance and mesophyll diffusion (Ferrell, 1970; Sestak et a1.1971; Zelitch, 1971). These, too, are to a great extent fixed by the genotype and, although subject to improved efficiency by breeding, they are not readily altered by manipulating environmental conditions. Several possibilities do exist, however, for extending the practical upper limit closer to the theoretical maximum by manipulating the environment and thereby accelerating seedling growth. CO_2 enrichment of the atmosphere and increased light intensity are specific examples that will be discussed later.

The Photosynthetic System

By photosynthetic system I mean the effec-tive mass of photosynthetic surface and its increment during ontogenetic development. Some overlap inevitably occurs when photosynthetic process and system are arbitrarily defined. I have nonetheless differentiated between them because the latter is more amenable to mani-pulation and control. For example, photo-synthetic production is not only limited by processes occurring within the chloroplasts,

but also by the number of chloroplasts and their rate of increase in the expanding mass of photosynthetic tissue. In other words, growth is a function both of the efficiency with which the photosynthetic system operates and with which the photosynthetic products are distributed throughout the plant to further increase the photosynthetic surface. Although it is the aim of both the researcher and the nurseryman to maximize the rate of increase of photosynthetic tissue, this increase can only be accomplished within the limits imposed by ontogenetic development.

Once endosperm reserves have been utilized, the seedling must subsist entirely on its own photosynthetic resources. For growth to ensue, an increase in the photosynthetic system must proceed through an orderly ontogenetic sequence that is maintained in balance with those of other essential plant systems. This orderly sequence is subject to rather rigid genetic control and the sequential stages cannot be circumvented. However, most species exhibit considerable plasticity, and the time required to pass through certain of these developmental stages can be accelerated by proper environmental control. Consequently, if an investigator is to approach the full growth potential of a seedling through rational experimentation, he must do so within the limitations imposed by ontogenetic development. It is because of this seemingly inextricable relation between ontogeny and environment that I am digressing to briefly survey the structure‾function relation of the ontogenetic sequence of seedling development before discussing the specific environmental factors under control of the investigator.

Limitations Imposed by Ontogenetic Development

A discussion of the upper limits of seedling growth brings to mind Blackman's (1919) "Compound interest law of plant growth." If we are to maximize growth rates during the seedling stage, then the mass of the photosynthetic system and that of all other systems subservient to it must increase exponentially, with each new increment of growth promoting a further increase in growth. Although the compound interest principle can serve a useful purpose in conceptualizing the growth process, we must remember that ontogenetic development, within which this principle must operate, is a highly complex series of events and that growth proceeds exponentially only when all events are fully synchronized. Thus, the investigator's imposition of the "wrong" level of control, or his untimely intervention during the "wrong" stage of ontogeny, can preclude achievement of the maximum growth potential.

One of the most critical periods in the life of a seedling is that time between depletion of food reserves in the seed and the emergence of functional, secondary foliage. Not only is this a critical period for seedling survival, but it is also a difficult one for accelerating growth. Once growth has been arrested for any reason during the post-germination or early seedling stages, it responds much more slowly to favorable growth conditions than at later stages of plant development (Milthorpe 1956). This is also a difficult period for accelerating growth because it requires the telescoping of many rate‾dependent processes. For example, the mere provision of new photosynthetic surface is not in itself a sufficient condition for accelerating growth if other tissue systems have not developed to a level where they can utilize the photosynthate rapidly.

The first photosynthetic organs to appear are the cotyledons, and their contribution initially supplements seed reserves (Marshall and Kozlowski 1974). Primary leaves soon follow, at which time seed reserves become depleted (Sasaki and Kozlowski 1968; 1970). It is a characteristic of primary leaves that they attain photosynthetic maturity quickly because seedling survival depends on their precocious productivity (Bormann 1958; Hadley 1965). Primary leaves can be increased in size and number, and consequently in photosynthetic productivity, by appropriate growth control (Lester 1967; Fowler 1961). Larger and more numerous primary leaves may in turn accelerate either the appearance and/or the size and vigor of the secondary leaves. The appearance of secondary leaves during the first season of growth is highly variable, and depends both on species characteristics and prevailing growth conditions.

Crucial to development of the vast continuum of ontogenetic events leading to accelerated photosynthetic productivity are the rates at which new foliage primordia are initiated at the apex and at which these primordia are induced to expand and to develop into functional leaves. Much has been written on the ontogenetii development of primary and secondary leaves and their axillary members in both gymnosperms (Bormann 1963; Allen and Owens 1972; Riding 1972) and angiosperms (Foster 1936; White 1955; Mogensen 1969). From these many writings and observations, it is clear that conditions for growth must be precisely balanced to main‾tain the production of new primordia at the apex. Seedling survival mechanisms are extremely delicate, and at any stage of ontogeny it is easy to set in motion physiological processes culminating in dormancy. Once a state of dormancy has become established in

the apex, it can be overcome only with diffi-
culty and after a lengthy delay.

The stem and its vasculature is often
considered part of the shoot (Wetmore and
Garrison 1966). Considering its ontogeny and
the processes that regulate vascular develop-
ment (Larson 1974), such a view is perhaps
acceptable. Nevertheless, certain factors of
the environment can be so manipulated that
either internode elongation is accelerated
(Wareing 1950) or stem diameter growth and
strengthening substantially increased (Borger
and Kozlowski 1973). Even though these
environmental conditions may be perceived by
or manifested through the foliar organs, it
is important that pertinent morphological
responses of the stem system be recognized
in maximizing growth.

While the foliar organs of the young
seedling are increasing in photosynthetic
capacity and the stem is increasing in size
and complexity, the roots are simultaneously
and synchronously developing to efficiently
perform their role. Like the foliar organs,
the emergent radicle derives its initial
sustenance from seed reserves, but subsequent
root growth depends wholly on photosynthates
produced by the leaves. Thus, the young
foliar organs must not only provide sufficient
food for their own development and the formation
of new foliar primordia at the apex, but also
for growth of the roots as well as the inter-
vening vascular system of the stem. Numerous
studies have shown that growth and development
of roots depend greatly on the aerial parts of
the seedling (Sutton 1969). This ontogenetic
relation is substantiated in part by obser-
vations on the periodic or intermittent growth
patterns of roots which appear to oscillate
in opposite phase to those of the foliar
organs (Hoffmann 1973).

The rhythmic growth of root and shoot may
be viewed as a series of feedback oscillations
that maintain a functional balance between
the root and shoot systems (Borchert 1973).
We know that trees do possess an efficient
homeostatic mechanism for maintaining a
balanced root/shoot ratio and for restoring it
following either a disturbance or exposure to
a stress situation (Wareing 1970). Because
of the prime importance of photosynthesis,
exposure to stress generally reduces shoot
growth before root growth, whereas release
from stress causes a resumption of shoot
growth before root growth (Loomis et al.1971).
Seedling root and shoot systems tend to be
capricious despite the opposing tendency of
the root/shoot ratio to attain homeostasis.
For example, in addition to a periodicity of
the root/shoot ratio in response to seasonal

growth patterns, either system may respond
suddenly and seemingly independently to changes
in the environment (Steinbrenner and Rediske
1964; Mooney 1972). If growth conditions are
favorable and food supplies adequate, root
growth may proceed more or less continuously
despite the close ontogenetic link between the
roots and foliar organs. Nurserymen attempting
either to maximize seedling growth or to mass-
produce nursery stock must consider the onto-
genetic relation between these two major plant
systems, for an unbalanced seedling will not
only limit growth potential but will also be
ill-suited for future out-planting.

In the foregoing paragraphs, I have but
briefly described the ontogenetic development
of a seedling. I cannot, however, overstress
its importance in maintaining accelerated,
exponential growth rates. If maximum growth
rates are to be attained, each ontogenetic
stage must proceed smoothly into the next, and
all systems must develop synchronously and in
proper balance. Ontogeny represents the
developmental series of events within which
either the investigator or the nurseryman must
continually operate. His success in accele-
rating seedling growth will be consistent with
the level of ontogenetic control that he is
capable of exercising. He must recognize that
factors of the environment not only influence
growth according to seedling development, but
that each factor influences growth in a
slightly different way. For example, long
photoperiods primarily increase node number
and internode length (Downs and Piringer 1958),
high light intensity promotes lateral branch
development (Krizek and Zimmerman 1973), and
temperature strongly influences the root/shoot
ratio (Kozlowski 1968a).

These are, of course, gross simplifications
and it must be borne in mind that each environ-
mental factor elicits a number of growth res-
ponses and that these responses further depend
on the interacting effects of all other pre-
vailing factors. The effects on growth and
ontogenetic development of the most important
environmental factors will be discussed in the
following sections.

MANIPULATING THE FACTORS THAT LIMIT GROWTH

So far I have consistently emphasized that
the ultimate factor limiting post-germination
seedling growth is the rate at which effective
photosynthetic surface increases. Within
limitations imposed by the ontogenetic sequence
of development, growth of each major system pro-
ceeds rhythmically with feedback mechanisms
maintaining homeostasis of the plant system as
a whole. However, there are numerous environ-

mental and cultural manipulations that can either shorten the rhythmic periods or telescope the ontogenetic stages.

In discussing these environmental factors and their manipulation in maximizing seedling growth rates, it might be helpful to re-intro- duce Blackman's (1905) principle of the "optima and limiting factors." We may extract two pertinent axioms from this principle: (1) The optimum level of a growth factor may fall well below the maximum level that can be tol- erated by the organism, and (2) when a number of different factors condition a growth pro- cess or function, the rate of the process will be determined by the factor that is most limiting. This principle is by no means totally applicable to accelerated growth and it must be used with caution (Kramer and Kozlowski 1960). Nevertheless, it may aid in sorting out subtly interacting factors that must of necessity be discussed separately.

Photoperiod

Photoperiod is perhaps the single, most important environmental factor that can be manipulated beyond the ambient range to accelerate seedling growth.   The morpho- genetic response of tree seedlings to a lengthened photoperiod may be either an increase in the number of foliar primordia, in the size of the foliar organs developing from these pri- mordia, in the length of internodes between the foliar organs, or in any combination of these (Wareing 1956; Downs and Borthwick 1956; Downs and Piringer 1958). Thus, long photo¯ periods telescope certain ontogenetic stages by accelerating both the appearance and development of the foliar organs. The increased foliar mass induced by long photoperiods, in combination with other favorable growth condi- tions, contributes to the photosynthetic system that in turn leads to accelerated, exponential growth rates.

The response of both conifer and hardwood species to a lengthened photoperiod is closely related to the normal seasonal growth pattern; that is, a longer photoperiod can modify the seasonal rhythm but cannot eliminate it. For example, in those conifers that normally grow by intermittent growth flushes, a period of apparent dormancy sets in following formation of the first terminal bud (Downs and Piringer 1958; Arnott 1974). However, this is only a transitory stage during which new primordia develop at the apex preparatory to further growth. It is also the stage, mentioned pre- viously, that is so sensitive to the environ- ment. If growth is arrested either during or following formation of the first terminal bud,

it can revert to a deep state of dormancy from which growth can only be resumed with difficulty.

Because the apex requires "temporary rest" for the production of new primordia, many species, including hardwoods, rest periodically and then resume apical growth even under long photoperiods (Lavarenne et al. 1971). Intermittent or rhythm- ic growth is less pronounced in species with indeterminate as opposed to determinate meri- stems. Thus, cottonwood seedlings continue to produce new primordia at regular intervals once secondary leaf production is underway (Larson and Isebrands 1971). Similarly, in white spruce (Pollard 1974) and a number of other conifers, the apex remains indeterminate for some time following germination. In some species, long photoperiods result in a pre- cocious transition from primary to secondary foliage, whereas in others, such as jack pine (Giertych and Farrar 1961), it appears that rapid growth prolongs the production of primary needles.

There is a critical daylength beyond which most species grow continuously (Downs and Borthwick 1956). Continuous growth in this sense allows for the intermittent flushes of growth due to new bud formation and bursting which may or may not become less frequent as the seedlings age. The critical daylength is apparently species-specific, although reports in the literature suggest that it invariably exceeds 16 hours (Wareing 1950; Downs and Piringer 1958; Fraser 1962; Hanover and Reicosky 1972). Short bursts of relatively low intensity light during the dark period are sufficient to induce the photoperiodic response (Arnott 1974). However, when long photoperiods are used to accelerate growth rates and to maximize growth, then light of higher intensities must be used throughout the entire light period (Krizek et al. 1970).

Light Intensity

Photoperiod may be thought of as a trig- gering mechanism for growth acceleration. However, photoperiod, or daylength, alone is insufficient for maintaining accelerated levels of seedling growth. Other growth requirements must also be optimized, particularly those directly related to building up the photo- synthetic system and utilizing it most effi- ciently. Thus, light intensities during the normal day as well as during the supplemental light period are of critical importance.

High light intensities promote photo- synthetic production by influencing both the photosynthetic process (Whiteman and Koller 1964; Mooney 1972) and the photosynthetic

system (Blackman 1956; Brix 1967). One of the reasons for the low efficiency of light utilization mentioned earlier is the self and mutual shading effects of the foliage. Self shading of a seedling's lower leaves by its own upper leaves and mutual shading of the intermingled leaves of adjacent seedlings can become limiting factors in closely grown containerized stock. High light intensities penetrate the canopy and expose the shaded lower and interior leaves to light values that more closely approach saturation intensities. A typical leaf becomes light-saturated at light intensities of about 10% to 20% full sunlight; that is, photosynthetic rate becomes independent of further increases in light intensity. Consequently, when light above the first layer of leaves is increased to exceed saturation intensities, light intensity within the next lower stratum of leaves is correspondingly elevated. The net effect is to diminish the influence of self and mutual shading and thereby increase photosynthetic rate of the entire plant (Hughes 1969). Zelawski et al. (1973) were able to increase light-saturation values and more closely approximate maximum photosynthetic efficiency by using a more evenly distributed diffuse light of high intensity that penetrated the seedling canopy from all sides. The bene⁻ fit of additional light in reducing effects of mutual shading can also be increased by maintaining a well-balanced nutrient supply, particularly nitrogen (Murata 1969).

The requirements for light and the tolerances to light of different intensities are highly variable both among species and during ontogenetic development of individual seedlings. Young pine seedlings with juvenile needles, for example, become light-saturated at intensities of 1500 to, 3000 ft⁻c, whereas older seedlings with some secondary needles require 2 to 3 times this light intensity for saturation (Bormann 1958; Hadley 1965). Young and mature leaves of yellow birch seedlings also differ markedly in their requirements for light saturation (Logan 1970). These variable requirements for light during seedling development must be con⁻ sidered in accelerated growth programs. For instance, it may be necessary to pre-condition seedlings of some species at relatively low light intensity during the earliest stages following germination and increase it as the seedlings age. It is essential, however, that the highest light intensity the seedlings can tolerate and still attain maximum growth rates should be maintained from the time of germination. In most cases, this will mean at or about light saturation.

Photosynthetic light saturation values for most forest trees are surprisingly low relative to full sunlight and surprisingly uniform among species. Data compiled by Lyr et al. (1967) showed that the maximum value for light saturation in both conifers and hardwoods ranged from about 1850 to 3200 ft⁻c. Most North American conifers also fall within this range (Walker et al. 1972). Interestingly, however, photosynthetic rates about 3/4 of the maximum were attained at light intensities of only 650 to 1390 ft-c (Lyr et al. 1967).

In spite of the apparent uniformity cited above, the wide range of values still permits considerable variability among species. In general, shade-intolerant species appear to be more efficient than shade-tolerant species at saturating light intensities (Leach 1967). Species also differ in their morphogenetic response to high light intensities. Several northern hardwoods, for example, grew tallest at 45% full light, but the greatest dry weights of both shoots and roots were accumulated by plants grown at light intensities above this level. Individual species, however, varied in response according to their shade-tolerance (Logan 1965). Shoot and root weights of several conifers also increased with increasing light intensity (Steinbrenner and Rediske 1964). One of the most marked morphogenetic influences of high light intensity is the stimulation of lateral branch growth (Krizek and Zimmerman 1973). Such stimulation illustrates the interacting effect of daylength and high light intensity, because long photoperiods are required for rapid initiation of the lateral bud primordia. The afore-mentioned morphogenetic responses pertain directly to the accelerated growth of containerized stock. It is perhaps more important to obtain a sturdy, well-balanced seedling for out-planting than simply a tall one.

Light intensity must be adapted to the species and to other conditions of growth. Light intensities beyond light saturation reduce growth (Krueger and Ferrell 1965), whereas excessively high light intensities can either injure or kill seedlings (Ronco 1972). Recent studies indicate, however, that relatively high-intensity light can be tolerated when used in combination with other highly optimum growing conditions, and that these conditions will result in remarkable increases in growth (Klueter et al. 1973; Anderson and Carpenter 1974).

For maximum photosynthetic productivity and growth, it is also essential that the highest possible light intensity be maintained during the supplemental light period. Although the photoperiodic response will occur at light intensities as low as 50 ft-c and for short exposures during the dark cycle, maximum benefit frequently requires a light intensity

capable of promoting photosynthesis. Consequently, for some species, it has been recommended that high light intensity be used throughout the long-day photoperiod from the time of germination (Krizek 1972).

To illustrate the effect of total light duration, Krizek and Zimmerman (1973) grew birch seedlings in a greenhouse under natural September sunlight supplemented with 200 ft-c fluorescent light to simulate a 16-hour day. Similar plants were grown in a growth chamber under a 2500 ft-c light intensity for the entire 16-hour day. Total radiation in the growth chamber was 270 langleys/16-hour day and in the greenhouse 58.7 langleys/11.24-hour mean daylength. All other conditions were maintained as identical as possible, At the end of 8 weeks from seed, the growth chamber seedlings were 6 times taller, had twice as many leaves, and produced lateral shoots containing 17 times as much dry matter as those in the greenhouse. Total radiation was the chief determinant of dry weight differences because other conditions were similar in both greenhouse and growth chamber.

Clearly, if we are to approach the upper limit of seedling growth we will need considerably more information, not only on the effects of high light intensity per se on photosynthetic production but also on the effects of total radiation and on the interacting effects of light intensity with other environmental factors.

Light Quality

In many respects, light quality is as important to the acceleration of seedling growth under controlled conditions as light intensity. Photosynthetically, plants are highly sensitive to spectral composition in weak light, but they become less so as light intensity increases (Nichiporovich 1967). The maximum quantum yield for photosynthesis is attained at two broad spectral peaks centered at 620 and 440 nm; the average height of the blue peak (440 nm) being about 70% that of the red (620 nm) (McCree 1972). Recent advances in lamp construction have now made it possible to attain high light intensities with optimum spectral composition for photosynthesis. These criteria can be met by high-intensity discharge lamps, such as the high-pressure sodium and metal halide lamps (Campbell et al. 1971; Bickford and Dunn 1972; Buck 1973).

Light quality is especially important during the supplementary part of the photoperiod. Although fluorescent light, rich in the red spectral component, will satisfy the photoperiodic requirement, maximum growth response only occurs when incandescent light, rich in the far-red spectral component, is also supplied (Downs and Borthwick 1956). For example, growth of pine seedlings was approximately doubled when incandescent was added to fluorescent light during the extended photoperiod (Downs and Piringer 1958). Best results are obtained when incandescent light comprises 10% to 20% of the total available light (Krizek et al. 1970; Buck 1973). Internode growth is further promoted if the supplemental incandescent light is supplied continuously and not just intermittently during the dark period (Cathey 1974).

Temperature

Low soil and air temperatures commonly limit seedling growth in both greenhouse and growth room environments (Krizek et al. 1970; Vogl et al. 1972). The effect of temperature becomes particularly noticeable in situations where other variables have been raised to optimum levels. For example, a high temperature is essential if maximum growth stimulation from CO enrichment is to be achieved (Krizek et al. 1968).

It is difficult to arrive at a temperature range for optimum seedling growth because of the numerous interacting variables existing in most test situations, and because of differences in species requirements. In general, however, overall seedling growth increases with increasing temperature to about 20° to 25°C and then declines (Downs and Borthwick 1956; Steinbrenner and Rediske 1964; Kozlowski 1968a; Tinus 1971; Hellmers and Rook 1973). To what extent this temperature range might be elevated by optimizing other environmental conditions is not known.

There is some evidence suggesting that the total heat sum, or heat requirement, may be a better criterion than absolute temperatures for determining the limiting effects of temperature on seedling growth (Hellmers 1962; Lanner 1964). Considerable evidence also indicates that many tree seedlings benefit from a thermoperiod, Best growth frequently occurs when the night temperature is about 12° to 13°C lower than the day, and it has been suggested that this differential may be as important to growth as the actual temperatures (Kramer 1958; Hellmers 1966).

The response to elevated temperatures depends to a large extent on the developmental state of the seedling. Since the relative growth response of shoots is generally

greater than that of roots, higher temperatures result in larger shoot/root ratios (Kozlowski 1968a; Hellmers and Rook 1973). Higher temperatures also bring about a redistribution of assimilates within the shoot, and this is expressed morphologically by reduced height growth and greatly increased foliage mass (Jensen and Gatherum 1965; Larson 1967). Brix (1967) interpreted a similar redistribution of growth in Douglas-fir in terms of Blackman's (1919) compound interest law. He observed that the increase in growth with a temperature rise from 13° to 18°C resulted from a temperature effect on total leaf area production, and not from a modified rate of photosynthesis per unit leaf area; that is, on the photosynthetic system and not on the photosynthetic process.

 Temperature modifies a host of metabolic reactions that are eventually expressed in measurable growth responses. Although some of the light reactions of photosynthesis are independent of temperature, rates of the dark reactions increase markedly with temperature (Heath 1969). This latter temperature response also applies to enzymatic reactions and to certain physiological processes that normally become rate-limiting at low temperatures.

Some plants can apparently adapt to high temperatures if other growth conditions are simultaneously raised above normal levels. The relatively heat-tolerant cucumber leaf, for example, exhibits a synergistic effect between temperature and light intensity. In a test chamber enriched with 1000 ppm CO_2, the optimum temperature for photosynthesis increased linearly 4°C for each 1000 ft-c increase in light intensity up to 6000 ft-c. At the conventional temperature of 24°C, light saturation occurred at 2000 ft-c. However, when temperature was raised to 36°C, light saturation was not reached until the intensity exceeded 8000 ft-c (Klueter et al. 1973). Although these data were obtained from a highly artificial experimental set-up, they nonetheless illustrate that optimal values for any given environmental factor are applicable only to the conditions described. Interactions with other factors can radically alter the "apparent optima" and further complicate efforts to attain the upper limit of growth.

CO2 Concentration

Earlier it was pointed out that the over-riding limiting factor for plant productivity was the efficiency of the photosynthetic process. Bonner (1962) placed the theoretical limit for the utilization of light energy at 20% and the upper limit under field conditions

at 5%. One of the most effective methods of increasing photosynthetic efficiency beyond the 5% limit is by CO_2 enrichment of the atmosphere (Pallas 1970; Ludwig 1972). Data suggest that the main effect of CO_2 enrichment is to decrease the sensitivity of the photosynthetic process to oxygen; that is, to suppress photo-respiration (Ludwig 1972). In tree seedlings, this means that high light intensities can be utilized more efficiently in a CO_2-enriched atmosphere resulting in increased net photosynthesis (Koch 1963) and greater dry weights (Yeatman 1970; Tinus 1972).

Koch's (1963) data nicely illustrate the interaction between CO_2 enrichment and light intensity in poplar seedlings. At ambient CO_2 concentrations, increasing light intensity had very little effect on the photosynthetic rate, but as CO_2 concentration was increased, the efficiency with which light was utilized increased dramatically. For example, at 2000 ppm CO_2 the rate of net photosynthesis was about 28 and 48 $mg/dm^2/hr$ for light intensities of 1850 and 5550 ft-c, respectively. When CO_2 concentration was raised to 4000 ppm, the photosynthetic rate increased to about 40 and 66 $mg/dm^2/hr$ for the same light intensities. Within the limits of the experiment, photosynthetic rate was increased more than fourfold by increasing CO_2 concentration from 350 ppm at a light intensity of 1850 ft-c to 4000 ppm at a light intensity of 5550 ft-c. It would be interesting to speculate as to whether a further synergistic increase could be achieved by simultaneously increasir temperature, as in the cucumber leaf experimc (Klueter et al. 1973) discussed earlier.

CO_2 enrichment of woody plants appears to be an overall growth stimulation, but the greatest measurable effect is on height growth (Hardh 1966; Funsch et al. 1970; Zimmerman et al. 1970; Siren and Alden 1972). For instance, at the end of 4 weeks, young crabapple seedlings grown in a growth chamber enriched with 2000 ppm CO_2 were 1.5 times taller than similar seedlings grown in a growth chamber at 400 ppm CO_2, and 3 times taller than those grown in a greenhouse at ambient CO_2 levels (Krizek et al. 1971).

CO_2 enrichment also reduces the growth depression due to mutual shading (Hughes 1969), and it appears equally effective on both sun and shade leaves (Logan 1970). These are important considerations for the rearing of containerized seedlings, because the required close spacings and the inevitable over-crowding result in appreciable self and mutual shading.

Soil Moisture are is undoubtedly one of the most difficult environmental factors to effectively maintain at optimum levels. Yet is is also one of the most critical limiting factors to seedling growth when either deficient or in excess. The effects of water on plant growth are well documented (Kozlowski 1968b) and I will consequently touch on just a few pertinent points.

When sufficient water is available, photosynthetic rates are largely determined by variations in temperature and light intensity (Hari and Luukkanen 1973). However, when soil moisture stress is impsed on seedlings the photosynthetic rate is imposed on seedlings the photosythetic rate is reduced sharply may not return to its original level for several days following release of the stress by watering (Polster abd Fuchs 1960). Low levels of soil moisture also retard the growth and maturation of roots (Sutton 1969) in addition to onterfering with water absorption and conducting capacity of the root system (Brix 1962). Excess moisture results in poor soil aeration, retarded root development,(Sutton 1969) and depressed photosynthesis (Jarvis and Jarvis 1963). Although these are generalizations and not universally applicable to all species i precisely the same manner, they do serve to illustrate the serious growth limitations that can ensue from poor or erratic soil moisture management. Large or prolonged fluctuations in soil moisture can largely negate the gains in accelerated seedlings growth obtained by optimizing other environmental conditions.

Fluctuations in soil moisture within reasonable limits do not greatly alter the seasonal growth patterns of seedlings, but they do reduce the absolute levels of growth (Lister et al. 1967). If too extreme, they may also cause seedlings to enter premature dormancy. Similarly, relative humidity of the air can materially reduce growth if it drops below 40% for a prolonged period (Krizek et al. 1970). In view of the difficulty in maintaining precise relative humidities, there is apparently little advantage to its control as long as it does not vary much beyond the range of 50% to 70% (Nitsch 1972).

Water quality and purity must be considered along with water availability. Freeman (1972) has listed numerous contaminants, both of natural origin and man-caused, that can seriously retard plant growth. Many of these are present in nursery watering systems and they can become particularly damaging if allowed to accumulate in the soil media. Control of both water quality and quantity are primarily engineering problems. In terms of accelerated seedling growth, the problem is maintaining them at adequate levels while other growth conditions are being optimized.

Mineral Nutrients

As in the case of soil moisture, adequate nutrient supplies are essential for maximum growth. Although there is still much to be learned, our knowledge of nutrition is sufficiently advanced that nutrient deficiencies should not limit accelerated growth. The nutrient requirements for seedlings of woody plants are well documented (Ingestad 1962; Mustanoja and Leaf 1965; Bengtson 1968), as are the soil requirements for containerization (McLean 1968; Matthews 1971; Owston 1973).

Russell (1972) has suggested three principal reasons to justify the sufficiency of this knowledge for growing plants in controlled environments:

(1) Existing fertilization techniques can assure adequate nutrient supplies if roots are provided with reasonably favorable environments.

(2) Rooting media can be provided in controlled environments that will not unduly restrict-root growth, thus nutrient uptake.

(3) When adequate nutrients are available for root growth, the rate at which nutrients are absorbed by roots is greatly influenced by the metabolic demand of the above-ground parts.

It is not my intention to under-estimate the importance of nutrients on seedling growth, for many nutrient and soil media-related problems can become serious limiting factors. These problems are a frequent cause for discussion among those growing containerized seedlings (Hitt 1971). However, research information is available to solve these problems, and application is primarily one of technology.

Other Limiting Factors

Wind, or air movement, is an important environmental factor that can, either by turbulent mixing or mechanical action, influence physiological processes such as photosynthesis (Caldwell 1970; Todd 1972), transpiration (Satoo, 1962), or the distribution

of photosynthates for growth (Larson 1965; Leiser et al. 1971). Some air movement should be provided in growth chambers (Krizek et al. 1970; Nitsch 1972), and perhaps in well-regulated greenhouses as well, to obtain the necessary mixing for uniform and maximum growth rates.

Insects and pathogens that either invade or infect tree seedlings can also become limiting factors to maximum growth if left unchecked. Again, however, methods are available for controlling these depredations, although the control itself may at times limit growth.

Finally, growth regulators should be mentioned. Endogenous hormones are involved at all levels of growth, and each growth response elicited by an environmental factor is mediated in some way by a hormone (Nitsch 1963; Osborne 1972). Exogenous hormones are being applied routinely to regulate the growth of selected crop plants and to increase the response to certain environmental factors. These growth regulators have found little application in the growth acceleration of woody plants. However, as time and growing space requirements for containerized seedlings become more critical, the demand for more information on these growth-promoting and growth- regulating chemicals will undoubtedly increase.

INTERACTIONS AND APPLICATIONS

It is clear that each of the foregoing environmental factors exerts a profound influence on seedling growth when varied independently. It is equally clear that each of the factors may exhibit an array of "apparent" optimal levels because of growth limitations imposed by other factors. Attainment of an array of "apparent optima" is undoubtedly due to synergistic interactions at more subtle levels within the seedling, because ultimately the growth-inducing influence of the environment is on specific hormonal and metabolic systems. Consequently, the upper limit of seedling growth can only be achieved when each factor has been brought to its "potential" optimum relative to that of each of the other factors. That is to say, maximum growth will ensue when the environment has pushed the genetic potential to its ultimate limit.

Although we have not yet reached the potential limit of seedling growth, we are gaining insight into ways in which the seedling's environment must be manipulated to approach it. Throughout this discussion, I have briefly described experimental situations illustrating the synergistic interactions that occur among some of the principal environmental factors. For example, it was pointed out that the photoperiodic response was greatly enhanced by increasing light intensity and by modifying spectral composition during the supplementary light period, and that light, temperature, and CO_2 concentration all interact so as to markedly increase light saturation. These interactions result not only in an exponential increase in the mass of tissue comprising the photosynthetic system, but also in a pronounced increase in the efficiency of the photosynthetic process. Finally, it was pointed out that all the environmental factors interact in turn with ontogenetic development of the seedling. Therefore, to attain maximum growth rates, allowance must also be made for probability that growth condition must be varied during seedling development.

There have been few attempts to optimize all environmental variables simultaneously. However, in those instances where preliminary trials have been conducted, the growth response has been spectacular (Zimmerman et al. 1970; Krizek et al. 1971). Data indicate that growth rates can be increased severalfold by shifting from outdoor nursery beds to a greenhouse, and still more by shifting from a greenhouse to moderately controlled growth chambers. All available evidence suggests that even greater increases in growth can be attained by rigidly controlling and optimizing all possible growth conditions. Investigation of both the requirements and the technology for the accelerated growth of crop plants has been progressing rapidly in recent years. Reports have appeared on systems for regulating CO_2 concentrations (Bailey et al. 1970), light intensity and quality (Campbell et al. 1971; Bickford an Dunn 1972; Buck 1973; Kimball 1973), as we ll as entire plant growth systems (Klueter e 1967; Krizek et al. 1968; 1970; Furuta 197 Nitsch 1972).

The main thrust of a growth acceleration program should be to produce a vigorous and hardy, plantable seedling in the shortest possible time. Siren and Alden (1972) suggest that plantable conifer seedlings can be produced in 8 to 12 weeks from seed. For some species this may be a realistic time scale, but for others it may be much too long and still others far too short. The requirements for accelerating seedling growth discussed in this paper are not presently applicable to the production of containerized seedlings for field planting. Nevertheless, it is only when the potential limit of growth has been defined by rigorous environmental control that it becomes possible to modify and scale down these conditions for the more practical problem

of mass production.

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Question: Is it possible that plants
grown under optimum conditions would experience
a shock when moved to field conditions, and
then actually grow slower than a tree that was
raised under less than optimum conditions?

Larson: Yes, this is entirely true. I
think it would be particularly so if the optimum
conditions had prevented setting of a good bud
prior to going into dormancy. This is the
reason we have a hardening off process, so that
seedlings can set a good bud before going
dormant.

Question: For many species of plants,
would high intensity artificial light be a
better source than sunlight for raising seed-
lings during the first few weeks or months of
life?

Larson: Yes. Artificial light may be
better than normal sunlight for the first few
weeks of growth. The reason we raise many
seedlings under shade is to control the natural
light intensity. By using artificial light,
you could control this even more critically.