Application of a PhotoThermal model for container-grown conifer seedling production

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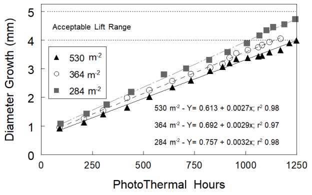

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Abstract

This study applied a total energy approach to model seedling growth for container-grown loblolly pine (*Pinus taeda* L.). Seedlings were grown in three container stocktypes representing a range of cavity volume and density patterns. These seedlings were grown under both controlled greenhouse and outside compound environmental conditions under well-defined cultural conditions. Models for temperature and light ranges were created from work on the ecophysiological performance and morphological development of loblolly pine to these atmospheric conditions. A PhotoThermal data set was created by generating hourly averages of these two environmental variables during the growing season. Light and temperature data were integrated, each weighted equally, into PhotoThermal hours (PT_H) to assess the crop growth response. Loblolly pine seedling growth in both the greenhouse and outside compound was directly related to PT_H. Seedling growth was also related to the container type with the largest cavity volume and lowest cavity density having the greatest growth per PT_H. Application of the PhotoThermal model is discussed for growing seedlings in an operational program having multiple production steps, delivery dates and nursery locations.

Keywords

PhotoThermal model; Container-grown seedlings; Loblolly pine; Operational applications

Contents

1 Introduction

Creation of optimum environmental conditions is critical for seedling development during their growth phase in a nursery production program. Two of the main atmospheric variables that drive seedling growth are light and air temperature. Light is the energy source for photosynthesis which turns this energy into carbohydrates, while temperature effects all metabolic processes which drive plant growth (Larcher 1995; Pallardy 2008). Understanding the interaction of these two atmospheric variables can provide a means to model seedling growth in the nursery. This allows one to look at energy inputs (i.e., lights & heat) versus costs and scheduling to determine economic feasibility and make operational decisions in relation to plant performance.

The heat summation approach has been used for over two centuries as a method for studying plant-temperature relationships (reviewed by Wang 1960). Growing Degree Days (GDD) is based on the method of describing plant-temperature relationships through the accumulation of daily temperatures above a certain threshold temperature (i.e., temperature above which plant growth starts) during the growing season. This GDD approach is a summation of the heat accumulation over time in relation to seasonal plant growth. This practice of heat summation has been used as a way to forecast plant development and thus scheduling (i.e. rate of growth versus projected timeframe of crop completion) of commercial agricultural crops (e.g. Boswell 1929; Magoon and Culpepper 1932; Madarmga and Knott 1951; Perry et al. 1986; Miller et al. 2001; Lee 2011) and forest nursery programs (e.g. Armson and Sadreika 1979; Hodgson 1985, 2015).

Wang (1960) and Perry et al. (1986) recommended that the following guidelines be considered in applying the heat unit approach to plant performance. First, the plant species threshold temperature (i.e., base temperature where plant growth slows to a negligible rate) should be based on the plant stage of development to be considered (e.g. germination, growth or fruit formation stage). Second, if possible, other important environmental parameters should be combined with temperature to obtain a more comprehensive environmental to plant response data set. Third, the range of measured environmental parameter(s) should be based on a logical framework for a defined plant development process.

Light is an environmental parameter also considered to sum in creation of a total energy unit approach. Daily light integral is the measured total photosynthetically active radiation (i.e. PAR) measured over a 24h period in a given location and can be used to define whole plant growth throughout the year (Korczynski et al. 2002). A daily light integral has been utilized in the horticulture industry to grow various plant species (e.g. Armitage and Wetzstein 1984; Graper and Healy 1991; Faust et al. 2005; Pramuk and Runkle 2005; Oh et al. 2009). Since light drives the plant's photosynthetic response and the derived photosynthate is the primary factor in seedling growth, it then seems logical that a daily light integral would be a useful variable to include in a total energy unit to quantify plant growth.

A total energy unit concept was first proposed by Nuttonson (1948; cited by Wang 1960). Various forms of a PhotoThermal parameter have been utilized to calculate crop development. Nix (1976) proposed the use of a PhotoThermal quotient for defining field crop growth; which was defined as the ratio of the daily mean irradiation to mean temperature. Islam and Morison (1992) considered this

PhotoThermal quotient to be meaningful in describing crop yields. Creation of a total energy unit approach was applied to grow horticulture crops under greenhouse conditions (Liu and Heins 1997, 2002; Niu et al. 2001; Moccaldi 2007). They developed the PhotoThermal ratio as the ratio of radiant energy (PAR) to thermal energy (degree days) to describe plant growth and development of greenhouse crops (Lui and Heins 2002). Sysoeva and Markovskaya (2006) proposed the inclusion of photoperiod length in a PhotoThermal model to ensure capturing the rate of development for plants that have photoperiodic sensitivity. The concept of PhotoThermal time, which is the product between GDD and hours of daylight time has examined timing of plant developmental stages (e.g. Robertson 1968; Angus et al 1981; Hammer et al. 1982; Masle et al. 1989; Li 2018). By applying various aspects of these conceptual guidelines, it is possible to create a total energy unit that could forecast development of container-grown conifer seedling crops.

This study applied an ecophysiological approach to create a total energy unit (i.e. PhotoThermal hour - PT_H) approach to model seedling growth for container-grown loblolly pine (*Pinus taeda* L.). The study objective was to determine whether PT_H based on the inherent physiological response patterns of loblolly pine seedlings to light and air temperature was capable of defining seedling growth produced as a range of stocktypes in containers having various cavity volumes and densities. Findings from this work were used to project seedling development under various light and temperature growing scenarios. The resulting model applied basic plant biology to improve operational nursery production decisions.

2 Materials and methods

2.1 Plant material

Loblolly pine (*Pinus taeda* L.) seedlings were grown to test the model. Two genotypes were used to create a test population. These genotypes were produced through somatic embryogenesis tissue culture protocols. These protocols have been developed over a 25-year period (Grossnickle et al. 1996) and was commercialized by CellFor Inc. for loblolly pine (Sutton et al. 2004; Denchev and Grossnickle 2019). Somatic germinants were transplanted into miniplugs (1cm W X 4cm D; rooting sponge, GrowTech Inc.) under cultural establishment protocols comparable to practices used in vegetative propagation programs (Dole and Gibson 2006; Denchev and Grossnickle 2019). Seedlings were grown in miniplugs until they were 5 cm in height, then transplanted into Styroblock containers (Beaver Plastics, Edmonton Alberta) of three stocktypes representing a range of cavity root volumes and density patterns used in container-grown seedling production programs (Table 1).

Seedlings were planted on Julian day 100 into a commercial growing media (2 parts sphagnum peat, 1 part grade 2 vermiculite, with perlite added at 10% of the mix). Seedlings were grown under two environmental regimes at a nursery in Central Saanich, British Columbia Canada (48°30’51”N, 123°23’2”W). Seedlings were grown in the greenhouse under the following atmospheric cultural practices: air temperature – vent to cool at 35 °C and heat at 5 °C, vapour pressure deficit (VPD) – 0.6 to 1.2 kPa with fog applied at >1.2 kPa, and light – ambient. Seedlings were also grown outdoors on raised pallets and exposed to spring and summer atmospheric conditions (i.e. full sunlight, air temperatures in the following ranges - Mean AVG 8.4 to 16.2 °C; High AVG 12.0 to 21.8

°C; Low AVG 3.8 to 10.7 °C and ambient VPD). The outdoor environment is defined as a cool summer Mediterranean climate (Köppen climate classification system). Greenhouse and outdoor grown seedlings had slightly different watering practices. Specifically, the greenhouse trial watered to saturation when container weights averaged 70% to 60% container capacity after dry down. The outdoor trial had water applied to saturation on a weekly basis or when container weights averaged >60% container capacity. All seedlings had a similar fertigation regime (i.e. 150 ppm N for 20-8-20 N-P-K with 30 mg l^{-1} micronutrients at every watering). Seedlings were assessed for nutrient analysis at the study midpoint and all treatments had optimal shoot tissue nutrient status (unreported data). Following standard shoot pruning practices for loblolly pine (Mexal and Fisher 1984), seedlings were shoot pruned at 10 cm and again at 20 cm to maintain shoot balance of 5 to 7 (H [cm] / DIA [mm]), that has been defined as a desirable sturdiness quotient value for conifer seedlings (Mexal and Landis 1990). Seedlings were grown until Julian Day 275 and had a finished height of 25 to 30 cm.

Table 1. Container stocktypes and dimension, and the number of loblolly pine seedlings grown in each container type during the testing of the PhotoThermal model.

Container type*	Cavities / tray	Cavity Depth (mm)	Cavity volume (cc)	Cavities m^{-2}	# of seedlings grown for greenhouse phase	# of seedlings grown for the outdoor phase
Superblock (415B)	112	148	108	530	1008	448
Superblock (412A)	77	116	125	364	1001	308
Superblock (512A)	60	119	220	284	960	240

*) Beaver Plastics Series Metric Description

2.2 Seedling measurements

Height and root collar diameter were measured weekly on 10 randomly selected seedlings per genotype in each container type. Height growth data was only used to monitor crop development, and not used in model validation due to shoot pruning practices. Each container type had their population of containers randomized after each weekly measurement period to minimize any edge effects. For seedling grown in the greenhouse, shoot mass and root mass were measured every three weeks, starting seven weeks after planting, on 10 randomly selected seedlings per genotype in each container type. Seedlings were harvested, dried for 48h at 80 °C, then weighed to determine shoot and root dry weights. It is recognized that seedling removal alters seedling cavity density patterns. To minimize this effect, care was taken to ensure a random selection of seedlings for removal was done from across containers for each tray density pattern. Across the trial, this required 10% to12% seedling harvesting and was done fairly evenly across all containers. Further, by midpoint of the trial, crown closure occurred across all container types, thereby mitigating any impact seedling removal had on altering the pattern of incoming solar radiation. After the trial mid-point, plug fill was assessed weekly on seedlings grown in the greenhouse. Plug fill was defined as the point when 10 seedlings from each genotype and stocktype could be extracted from the container and retain their media-root system structural integrity (i.e., extracted seedling held horizontal with plug integrity maintained). Morphological data collected for the two genotypes showed no significant difference in growth response (data not reported). This allowed data to be pooled when defining seedling growth in relation to PhotoThermal hours.

2.3 PhotoThermal model

In applying an ecophysiological approach to create the PhotoThermal hour (PT_H) to describe loblolly pine growth, temperature and light ranges were based on reported work of the physiological performance and morphological development of loblolly pine seedlings to atmospheric conditions. These ranges were defined as: temperature range of 4 to 48 ^{o}C, and light levels from dark up to full sunlight (i.e. 0 to 2,000 μmol m^{-2} s^{-1}). These were the potential temperature and light ranges loblolly pine seedlings are typically exposed to during the growth phase of nursery crop production. The photosynthetic response curve to light of loblolly pine seedlings from Teskey et al. (1987) was used to model plant growth response to light. A similar pattern was also reported for this species by Kramer and Decker (1944) and Kozlowski (1949). The photosynthetic response curve to light was used to model seedling growth because these data presented a full range physiological response pattern for loblolly seedlings (Figure 1A). This approach is supported by work showing loblolly pine seedling seasonal net assimilation rates (capturing light intensity and duration responses of photosynthesis) were significantly correlated to seedling growth (Ledig and Perry 1969). Furthermore, loblolly pine seedlings show a similar pattern for root growth (Barney 1951) and total dry mass (Shirley 1929) as sunlight increases from zero to full sunlight. The temperature model, was created for loblolly pine based on findings from a series of scientific papers (Barney 1951; Kramer 1957; Teskey et al. 1987; Teskey and Will 1999; Sword-Sayer et al. 2005) with combined data defining loblolly pine growth in relation to temperature. Data from all temperature response trials were normalized to allow for the creation of temperature portion of the growth model (Figure 1B). This allowed for creation of a loblolly pine seedling temperature driven growth model when all other environmental variables were considered optimum.

To integrate light and temperature data into one parameter requires that environmental parameters be reduced to a common unit and each weighted equally to define the crop response. Thus, temperature and light plant response to these environmental parameters were calibrated as net growth and net photosynthesis, respectively, as a percentage of maximum response (i.e. scale of 0 to 1) (Figure 1). This allowed for the generation of a common value unit for both light and temperature response from their separate models; which were combined to create a single total energy unit.

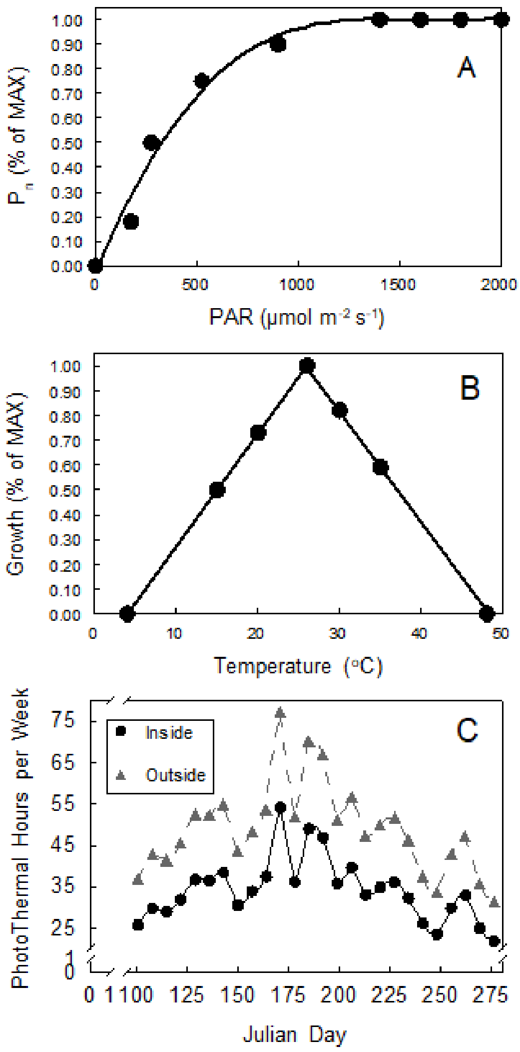

Figure 1. The combination of the light and temperature models having common units allowed for the creation of a singular PhotoThermal unit combining light and temperature response for loblolly pine. A) The light portion of the PhotoThermal model (- 4E-07PAR^2 + 0.001PAR + 0.1) was derived from the net photosynthesis response curve for loblolly pine (Teskey et al. 1987). B) The temperature portion of the model was created for loblolly pine based on findings from a series of scientific papers (Barney 1951; Kramer 1957; Teskey et al. 1987; Teskey and Will 1999; Sword-Sayer et al. 2005) that combined data to define loblolly pine growth in relation to temperature. Data from all temperature trials were normalized to allow for the creation of temperature portion of the growth model (T<=26, (0.0455*T-0.1818); T>=26, (2.1818-0.0455*T)]). C) Describes the weekly accumulation of PhotoThermal hours during the growing season for seedling locations both inside the greenhouse and in the outside compound next to the greenhouse.

The PhotoThermal data set was created in the following manner. First, light and temperature data, measured at seedling height, were taken every 5 minutes from the greenhouse and outside environment using a monitoring system (Argus Controls www.arguscontrols.com) to generate hourly averages of these to environmental variables. A PhotoThermal value was assigned to each hour (PT_H) when the crop was growing by taking average hourly light and temperature readings, comparing these values to their respective models (Figure 1 A&B) and creating a common value unit for each of these two environmental variables. A PT_H unit value was defined for each hour of the day as the product of LIGHT * TEMPERATURE with an equal weighting for each atmospheric variable. With this approach whenever it was dark a PT_H was recorded as a zero. A PT_H data set was created for this trial from Julian day 101 through Julian day 275 (Figure 1C). The PT_H data set shows that the outside compound, compared to the within greenhouse data set, had a greater weekly PT_H accumulation; which was due, in part, to a 30% light extinction from the greenhouse structure.

The PhotoThermal model was tested for the exponential growth phase when seedlings are grown to ensure rapid development to meet a defined shoot size and plug fill under the controlled greenhouse and outside environment. Thus, growth data collected at weekly intervals was related to accumulated PT_H data, through regression analysis, to define the seedling growth rate. The model was designed to answer the question of how much PhotoThermal energy was required to grow a seedling to a defined plant size. The model was not tested during seed germination and initial plant establishment phase or during the hardening phase for transition to lifting, possibly storage and shipment to the field.

3 Results and discussion

3.1 Growth to PhotoThermal hours (PT_H)

Loblolly pine seedling growth in the greenhouse was directly related to PT_H. Seedling shoot growth (i.e. diameter and shoot dry weight) was directly related to PT_H (Figure 2 A & B, respectively), with the growth rate per PT_H, for each stocktype, defined by the dependent variable in regression models. Height growth was not assessed in relation to growth per PT_H in this finished seedling trial due to shoot pruning cultural practices, though previous work has reported a strong relationship for height growth per PT_H for loblolly pine miniplug seedlings (Denchev and Grossnickle 2019). A number of studies looking at growing horticulture crops under greenhouse conditions have reported that shoot development can be directly related to the combined amount of light and temperature conditions provided during the plant growth phase (Lui and Heins 2002; Pramuk and Runkle 2005; Moccaldi and Runkle 2007). Loblolly pine seedling root growth was also directly related to PhotoThermal hours (Figure 2C). This shows that total seedling morphological development was related to PT_H, thus enabling the use of a total energy unit approach to monitor loblolly pine seedling growth under greenhouse conditions.

Loblolly pine seedlings grown in the outside environment had diameter growth directly related to PT_H (Figure 3). Outside grown seedlings diameter growth rate was 39% to 45% slower per PT_H, across container types, than seedlings grown in the greenhouse. Even though seedlings grown outside had a greater exposure to light, the lack of complete control of their plant water balance (i.e., water uptake & loss) probably explains the limited seedling growth. This lack of control of their water balance meant that seedlings grown outside were exposed to drier conditions; which is dictated by the combination of lower available soil water and a wider range of VPD conditions (Larcher 1995). Water stress occurs in trees when their water deficit, reaches a level which negatively affects their physiological processes (Teskey and Hinckley 1986). Under high levels of available soil water, stomata are open (Lassoie et al. 1985), photosynthetic levels are high (Kozlowski et al. 1991) and there is optimum plant growth (Hsiao 1973). In this trial, outside grown, compared to greenhouse grown, seedlings had a watering regime that allowed for a slightly drier container media. This watering regime could have created occasional periods of moderate plant water stress which can reduce seedling growth (Kozlowski 1982; Grossnickle 2000). In addition, inside VPD conditions were controlled to create an ideal growing environment (i.e. 0.6 to 1.2 kPa), whereas outside VPD conditions were allowed to fluctuate in response to ambient summer conditions. Seedlings grown outside were exposed to cool summer Mediterranean climate summer VPD conditions of the Pacific Northwest where the ambient VPD can range from 1.0 to 5.0 kPa (Grossnickle and Russell 1991; Major et al. 1994). A decline in P_n as VPD increases is a typical pattern for loblolly pine (Teskey et al. 1986) and conifer species in general (Kozlowski et al 1991; Grossnickle 2000). A slightly drier watering regime in combination with a greater range of VPD conditions were probably the main reasons seedlings grown outside required a greater number of PT_H to achieve the same level of shoot development as greenhouse grown seedlings.

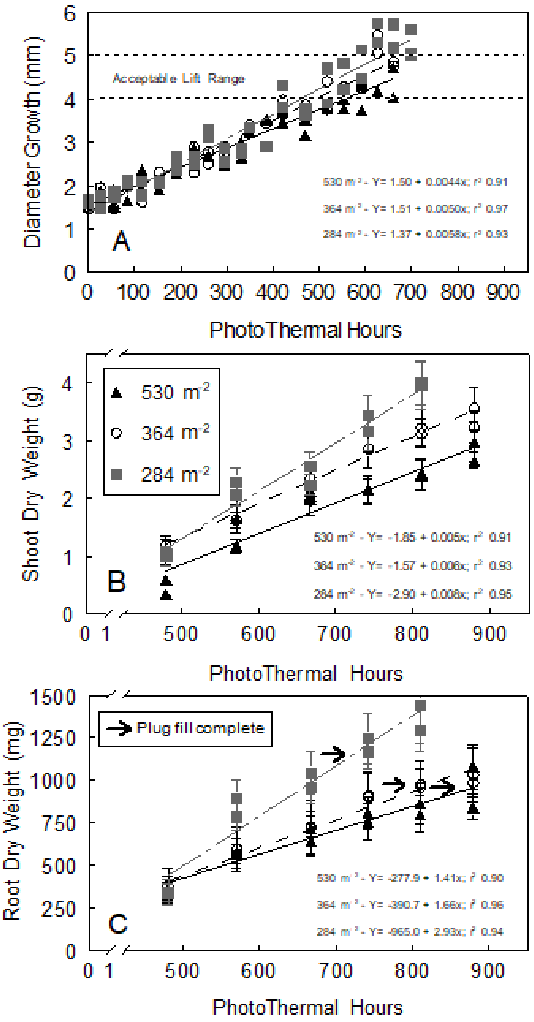

Figure 2. Loblolly pine seedling growth across the spring/summer growing season inside the greenhouse in relation to PhotoThermal hours. Seedling growth was defined across three container cavity density patterns (530, 364 & 284 m^{-2}) for: A) diameter (n= 20 – SE not shown because typically smaller than symbol size), B) shoot dry weight, and C) root dry weight (n= 20 +/- SE). Completed plug fill (n= 20) was defined to indicate when the root development provided for plug integrity when extracted from the container cavity.

Nevertheless, loblolly pine seedling growth was directly related to PT_H, whether seedlings were grown in the greenhouse (Figure 2) or outside (Figure 3). In the energy model proposed by Liu and Heins (1997) for greenhouse horticultural crops, they quantified light (PAR) as the daily light integral (mol m^{-2} d^{-1}) to thermal energy as daily thermal time (degree-days d^{-1}) and used this approach to describe plant growth (Lui and Heins 2002). The PhotoThermal model applied in this current study takes a slightly different approach. First, species specific physiological models were created to define loblolly pine seedling response to both light and temperature. Second, rather than quantify energy values as daily averages, hourly data was used to create a PT_H value; which could then be summed over the entire seedling growth phase. The result was the creation of a PhotoThermal model that was capable of defining the growth phase of loblolly pine seedlings. Both Liu and Heins (1997) and PT_H approaches effectively define plant growth in relation to light and thermal energy. The difference is that the PhotoThermal model provides a degree of refinement with growth based on species specific ecophysiological patterns in relation to a direct measurement of hourly energy inputs.

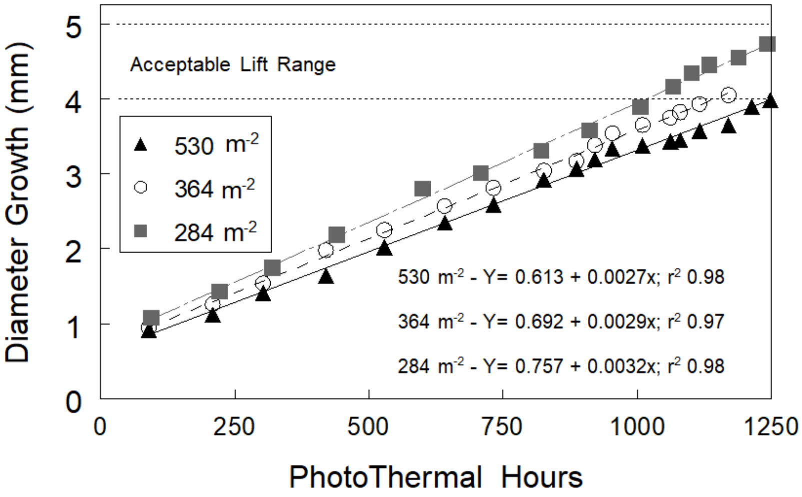

Figure 3. Loblolly pine seedling growth across the spring/summer growing season in the outside compound in relation to PhotoThermal hours. Seedling diameter growth (n= 20 – SE not shown because typically smaller than symbol size) was defined across three container cavity density patterns (530, 364 & 284 m^{-2}).

3.2 Growth to PT_H and cavity density-volume effects

Both shoot and root growth were related to cavity density patterns. For greenhouse grown seedlings, diameter growth at the lowest density (284 cavities m^{-2}) grew at a 16% and 32% faster rate than seedlings grown at a density of 364 cavities m^{-2} and 530 cavities m^{-2}, respectively (Figure 2). This meant that seedling diameter growth reached 4 mm in size at 455, 493 and 559 PT_H for a density of 284 cavities m^{-2}, 364 cavities m^{-2} and 530 cavities m^{-2}, respectively. For outside grown seedlings diameter growth at the lowest density (284 cavities m^{-2}) grew at a 10% and 18% faster rate than seedlings grown at a density of 364 cavities m^{-2} and 530 cavities m^{-2}, respectively (Figure 3). For greenhouse grown seedlings shoot and root dry weights of seedlings grown at the lowest density (284 cavities m^{-2}) showed shoot weight to increase at a 33% and 60%

faster rate, and root weight to increase at a 76% and 108% faster rate than seedlings grown at a density of 364 cavities m^{-2} and 530 cavities m^{-2}, respectively (Figure 2). This increase in root development for seedling grown in the lowest density (284 cavities m^{-2}) resulted in plug fill occurring after exposure to 700 PT$_H$, whereas it required 780 and 850 PT$_H$ for plug fill to occur for seedlings grown at a density of 364 cavities m^{-2} and 530 cavities m^{-2}, respectively.

There is a cavity density effect when growing container-grown seedlings. A number of studies have reported that a higher cavity density limits conifer seedling growth (Timmis and Tanaka 1976; Simpson 1991; Simpson 1994; Jinks and Mason 1998; Aphalo and Rikala 2003; Aghai et al. 2014). This phenomenon of greater cavity growing density limiting seedling growth has also been reported for loblolly pine (Barnett and Brissette 1986). Thus, cavity density within the container tray has a direct effect on final seedling size.

A confounding effect of container growing has been reported with cavity volume in relation to cavity density; at low cavity densities lower cavity volume reduced root growth by limiting water and mineral uptake capacity (Tschaplinski and Blake 1985; Will and Teskey 1997), thereby influence seedling growth (e.g. Scarratt 1972; Hocking and Mitchell 1975; Jinks and Mason 1998). Plug fill occurred more rapidly in containers with the greatest cavity volume and lowest cavity density (220 cc cavity volume for 284 cavities m^{-2}) compared to later plug fill for seedlings grown at a smaller cavity volume and greater cavity density (i.e. 125 cc cavity volume for 364 cavities m^{-2} and 108 cc cavity volume for 530 cavities m^{-2}). This indicated that larger cavity volumes, in low cavity density trays, have potential root restriction earlier in the growth cycle than lower cavity volumes in high cavity density trays. A well-defined watering regime applied water to all container types at the same defined container capacity, thereby minimizing any water stress. And, optimum fertilization resulted in no difference in nutritional status between seedlings from different container types; which was similar to reported findings of Aphalo and Rikala (2003). This shows cultural practices applied in this study minimized cavity volume as a confounding effect on seedling growth.

As loblolly pine seedlings reached 10 to 15 cm in shoot height, crown closure started to occur first at higher cavity densities. Container cavity density becomes critical for loblolly pine seedling biomass accumulation as the growing season lengthens (Barnett and Brissette 1986). As a result, diameter growth started to slow after 300 PT$_H$ for seedlings grown at higher cavity densities (Figure 2A). Here, cavity density limited seedling access to incoming solar energy as needles of adjacent seedlings started to shade foliage, thus limiting photosynthesis and slowing growth. Over the growing season, seedlings grown at higher within container cavity densities received less incoming solar radiation (i.e., use of available PT$_H$), thus had less shoot and root development, compared to seedlings grown at lower cavity densities, for the same timeframe in the nursery. The effect of cavity density on light competition in a container-grown seedling program is considered the most important factor influencing seedling growth (Simpson 1991) because canopy density alters growth primarily through shading (Aphalo and Ballare´ 1995). This phenomenon of light competition in relation to cavity density was the major reason for differences in loblolly pine seedling growth in the tested container stocktypes.

3.3 PhotoTermal model application to operational nursery programs

This PhotoThermal model was used operationally in the production of both miniplug and finished seedlings by CellFor Inc. to grow loblolly pine seedlings produced from a somatic embryogenesis tissue culture propagation program (Denchev and Grossnickle 2019). Growing loblolly pine seedlings to defined sizes required shipment of plants throughout the year, with miniplug and, bareroot and container-grown seedling nursery production programs conducted at a number of locations that spanned across North America (i.e., Pacific Northwest, Southwest, Great Lakes, Mid-Atlantic, Southeast regional locations) that had different seasonal temperature (e.g. https://www.ncdc.noaa.gov/ customer-support/ partnerships/ regional-climate-centers) and light regimes (Korczynski et al. 2002). Depending upon availability of localized temperature and light data related to the nursery location, environmental data sets of hourly, daily, weekly or monthly values were utilized in producing potential growth scenarios from the PhotoThermal model. These potential growth scenarios utilized regional historical temperature and light data for various nursery locations. This allowed management to utilize PhotoThermal model seedling growth projections to make decisions on when to ship plant material from the lab to the miniplug nurseries, from the miniplug nursery to the bareroot and container-grown seedling nurseries, and then define when full-sized seedlings would be ready to ship to the customer.

An example of PhotoThermal model application in container-grown seedling program planning is shown in Table 2. In this scenario the PhotoThermal hours across the growing season for a proposed nursery location were defined. The model output allowed one to project the required length of time to grow a finished seedling to a diameter of 4.0 to 4.5 mm for a specific stocktype (e.g. cavity density of 364 m^{-2}) with a defined starting plant material (e.g. miniplug seedlings with a root collar diameter of 1.0 mm and height of 6 cm). Model results defined how long it took to grow a container-grown finished seedling to the desired diameter size depending on the plant week. This allowed the nursery operation to make decisions on when to move miniplug seedlings into the finished seedling nursery during the first half of the year and produce seedlings with desired morphological development at various dates by the end of the year.

The PhotoThermal model allowed miniplug and finished seedling nursery production cycles to become integrated with the annual lab production of tissue culture germinants, thereby ensuring the production of full-size seedlings with morphological specifications that ensured good field performance after outplanting (Denchev and Grossnickle 2019). The model became an essential part of the nursery planning program as the production cycle scaled into the 10s of millions of germinants and miniplug seedlings being produced in a continuous yearly cycle, and then integrated into a finished seedling program at bareroot and container-grown seedling nurseries where the planting window spanned from late winter through spring. The PhotoThermal model became a tool that enabled the operations of lab and nursery production cycles to integrate basic plant biology with site environmental conditions to create a system that ensured an even flow of plant material through the entire plant production program.

Table 2. PhotoThermal model scenario for growing container-grown finished loblolly pine seedlings in an open nursery compound in Georgia USA (31°10’N 83°47’W – Insert photograph of the open nursery growing facility) when planted over the late winter and spring planting season (i.e. plant week). The seasonal average PhotoThermal hours (AVG PT$_H$) for this location were determined for a four-year timeframe for each growing week. This model scenario projects that 1,000 to 1,200 PTH (green shaded section under each plant week) are required to grow a finished seedling to a diameter of 4.0 to 4.5 mm at a cavity density of 364 m^{-2} with a defined starting plant material (e.g. miniplug seedlings with a root collar diameter of 1.0 mm and height of 6 cm); with the growth rate based on the 364 m^{-2} cavity density model in Figure 3.

Growing Week	AVG PT$_H$	Plant Week								
		10	12	14	16	18	20	22	24	26
10	32	32								
11	36	68								
12	42	111	42							
13	38	149	81							
14	40	189	120	40						
15	49	238	170	89						
16	53	291	222	142	53					
17	51	342	273	193	104					
18	55	397	328	248	159	55				
19	58	455	387	306	217	113				
20	54	509	441	360	271	168	54			
21	61	570	502	421	332	228	115			
22	52	622	553	473	384	280	167	52		
23	56	678	610	529	440	336	223	108		
24	56	734	666	585	496	392	279	164	56	
25	58	792	724	643	554	450	337	222	114	
26	55	847	779	698	609	506	392	277	169	55
27	56	904	835	755	666	562	449	334	226	112
28	53	957	889	808	719	615	502	387	279	165
29	54	1011	943	862	773	670	556	441	333	219
30	55	1066	998	917	828	724	611	496	388	274
31	51	1117	1048	968	879	775	662	547	439	325
32	52	1168	1100	1019	930	826	713	598	490	376
33	52	1220	1152	1071	982	878	765	650	542	428
34	50		1202	1121	1032	929	815	700	593	478
35	51			1172	1083	979	866	751	643	529
36	50			1222	1133	1029	916	801	693	579
37	49				1183	1079	966	850	743	628
38	47				1229	1125	1012	897	789	675
39	46					1171	1058	943	835	721
40	42					1213	1100	985	877	763
41	36						1136	1021	913	799
42	41						1176	1061	953	839
43	33						1210	1094	987	872
44	34							1128	1021	906
45	29							1158	1050	936
46	25							1182	1075	960
47	18							1200	1092	978
48	14								1106	992
49	12								1119	1004
50	12								1131	1016
51	9								1140	1025
52	16								1155	1041

4 Conclusion

The PhotoThermal model was designed to apply the basic understanding of energy inputs of light and heat that are required to grow loblolly pine seedlings. Specifically, these energy inputs in relation to the growth of loblolly pine were defined and then synthesized to create a PT$_H$ which is a total energy unit. This PT$_H$ provided an ecophysiological approach to model growth for both miniplug (Denchev and Grossnickle 2019) and container-grown loblolly pine seedlings. The PhotoThermal model allowed lab operations and nursery production cycles to be synchronized by understanding the timeframe it took to grow target miniplug and finished seedlings throughout the year. The operational outcome was that the PhotoThermal model became a planning tool to manage seedling crop production based on the application of loblolly pine seedling ecophysiological patterns with seasonal light and temperature regimes for nurseries located at various North American regional locations.

5 References

Aghai MM, Pinto JR, Davis AS (2014) Container volume and growing density influence western larch (*Larix occidentalis* Nutt.) seedling development during nursery culture and establishment. New For 45:199-213. https://doi.org/10.1007/s11056-013-9402-8

Angus JF, Mackenzie DH, Morton R, Schafer CA (1981) Phasic development in field crops II. Thermal and photoperiodic responses of spring wheat. Field Crops Res 4:269-283. https://doi.org/10.1016/0378-4290(81)90078-2

Aphalo PJ, Ballare CL (1995) On the importance of information-acquiring systems in plant–plant interactions. Funct Ecol 9:5-14. https://doi.org/10.2307/2390084

Aphalo P, Rikala R (2003) Field performance of silver-birch planting-stock grown at different spacing and in containers of different volume. New For 25:93-108. https://doi.org/10.1023/A:1022618810937

Armitage AM, Wetzstein HY (1984) Influence of light intensity on flower initiation and differentiation in hybrid geranium [*Pelargonium* X *hortorum*, irradiance]. HortSci 9:114-116.

Armson KA, Sadreika V (1979) Forest tree nursery soil management and related practices. Ontario Ministry of Natural Resources, Toronto, ON.

Barnett JP, Brissette JC (1986) Producing southern pine seedlings in containers. USDA forest service general technical report SO-59, p 71. https://doi.org/10.2737/SO-GTR-59

Barney CW (1951) Effects of soil temperature and light intensity on root growth of loblolly pine seedlings. Plant Physiol 26:146-163. https://doi.org/10.1104/pp.26.1.146

Boswell VR (1929) Factors influencing yield and quality of peas. Maryland Agric. Exp. Sta. Bul. 306.

Denchev P, Grossnickle SC (2019) Somatic embryogenesis for conifer seedling production. Reforesta 7:109-137. https://doi.org/10.21750/REFOR.7.08.70

Dole JM, Gibson JL (eds) (2006) Cutting propagation: A guide to propagating and producing floriculture crops. Ball Publishing, Batavia IL.

Faust JE, Holcombe V, Rajapakse NG, Layne DR (2005) The effect of daily light integral on bedding plant growth and flowering. HortSci 41:114-119. https://doi.org/10.21273/HORTSCI.40.3.645

Graper DF, Healy W (1991) High pressure sodium irradiation and infrared radiation accelerate Petunia seedling growth. J Amer Soc Hort Sci 116:435-438. https://doi.org/10.21273/JASHS.116.3.435

Grossnickle SC (2000) Ecophysiology of northern spruce species: the performance of planted seedlings. NRC Research Press, Ottawa.

Grossnickle SC, Russell JH (1991) Gas exchange processes of yellow-cedar (*Chamaecyparis nootkatensis*) in response to environmental variables. Can J Bot 69:2684-2691. https://doi.org/10.1139/b91-337

Grossnickle SC, Cyr D, Polonenko DR (1996) Somatic embryogenesis tissue culture for the propagation of conifer seedlings: a technology comes of age. Tree Planters' Notes 47:48-57.

Hammer GL, Goyne PJ, Woodruff DR (1982) Phenology of sunflower cultivars. III. Models for prediction in field environments. Aust J Agric Res 33:263-274. https://doi.org/10.1071/AR9820263

Hodgson TJ (1985) Heat unit summation theory in commercial nursery management. In: South DB (ed) Proceedings, International symposium on nursery management practices for the southern pines. Auburn, AL: Auburn Univ. pp. 64-71.

Hodgson TJ (2015) The Use of Remote Monitoring and Growing Degree Days for Growing Container Seedlings. Tree Planters' Notes 58:78-80.

Hocking D, Mitchell DL (1975) The Influences of Rooting Volume–Seedling Escapement and Substratum Density on Greenhouse Growth of Lodgepole Pine, White Spruce, and Douglas Fir Grown in Extruded Peat Cylinders. Can J For Res 5:440-451. https://doi.org/10.1139/x75-061

Hsiao TC (1973) Plant response to water stress. Annu Rev Plant Physiol 24:519-570. https://doi.org/10.1146/annurev.pp.24.060173.002511

Islam MS, Morison JIL (1992) Influence of solar radiation and temperature on irrigated rice grain yield in Bangladesh. Field Crops Res 30:13-28. https://doi.org/10.1016/0378-4290(92)90053-C

Jinks R, Mason B (1998) Effects of seedling density on the growth of Corsican pine (*Pinus nigra* var. *maritima* Melv.), Scots pine (*Pinus sylvestris* L.) and Douglas-fir (*Pseudotsuga menziesii* Franco) in containers. Ann For Sci 55:407-423. https://doi.org/10.1051/forest:19980402

Korczynski PC, Logan J, Faust JE (2002) Mapping monthly distribution of daily light integrals across the contiguous United States. HortTech 12:12-16. https://doi.org/10.21273/HORTTECH.12.1.12

Kozlowski TT (1949) Light and water in relation to growth and competition of Piedmont forest tree species. Ecol Mono 19:207-231. https://doi.org/10.2307/1943536

Kozlowski TT (1982) Water supply and tree growth. Part I. Water deficits. For Abstr 43:57-95.

Kozlowski TT, Kramer PJ, Pallardy SG (1991) The physiological ecology of woody plants. Academic Press, New York. https://doi.org/10.1016/B978-0-12-424160-2.50005-7

Kramer PJ (1957) Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. For Sci 3:45-55.

Kramer PJ, Decker JP (1944) Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. Plant Physiol 19:350-358. https://doi.org/10.1104/pp.19.2.350

Larcher W (1995) Physiological plant ecology: Ecophysiology and stress physiology of functional groups. 3rd Edition, Springer, Berlin.

Lassoie JP, Hinckley TM, Grier CC (1985) Coniferous forests of the Pacific Northwest. In: Chabot BF, Mooney HA (eds) Physiological ecology of North American plant communities. Chapman and Hall, NY, pp. 127-161. https://doi.org/10.1007/978-94-009-4830-3_6

Ledig FT, Perry TO (1969) Net assimilation rate and growth in loblolly pine seedlings. Forest Sci 15:431-438.

Lee C (2011) Corn growth stages and growing degree days: a quick reference guide. AGR 202. Lexington, KY: Cooperative Extension Service, University of Kentucky, College of Agriculture. http://www2.ca.uky.edu/agc/pubs/agr/agr202/agr202.pdf.

Li X, Guo T, Mu Q, Li X, Yu J (2018) Genomic and environmental determinants and their interplay underlying phenotypic plasticity. PNAS, 115:6679-6684. https://doi.org/10.1073/pnas.1718326115

Liu B, Heins RD (1997) Modeling poinsettia vegetative growth and development: The response to the ratio of radiant to thermal energy. II Modelling Plant Growth, Environmental Control and Farm Management in Protected Cultivation 456, pp.133-142. https://doi.org/10.17660/ActaHortic.1998.456.15

Liu B, Heins RD (2002) PhotoThermal Ratio Affects Plant Quality in: Freedom Poinsettia. J Am Soc Hort Sci 127: 20-26. https://doi.org/10.21273/JASHS.127.1.20

Madarmga FJ, Knott JE, (1951) Temperature summations in relation to lettuce growth Proc Am Soc Hort Sci 58:147-152.

Magoon CA, Culpepper CW (1932) Response of sweet corn to varying temperatures from time of planting to canning maturity. USDA Tech Bull 312.

Major JE, Grossnickle SC, Arnott JT (1994) Influence of dormancy induction treatments on the photosynthetic response of field planted western hemlock seedlings. For Ecol Manage 63:235-246. https://doi.org/10.1016/0378-1127(94)90113-9

Masle J, Doussinault G, Farquhar GD, Sun B (1989) Foliar stage in wheat correlates better to PhotoThermal time than to thermal time. Plant Cell Environ 12:235-247. https://doi.org/10.1111/j.1365-3040.1989.tb01938.x

Mexal JG, Fisher JT (1984) Pruning loblolly pine seedlings. In: Proc. South. Nur. Conf. USDA For Ser, Southern Reg, Atlanta, Georgia. pp. 75-83.

Mexal JG, Landis TD (1990) Target seedling concepts: height and diameter. In: Rose R et al. (eds) Target seedling symposium: Proceedings of the combined meeting of western forest nursery association. USDA forest service general technical report RM-200, pp. 17-36.

Miller P, Lanier W, Brandt S (2001) Using growing degree days to predict plant stages. MT2001103 AG. Missoula, MT: Montana State University Extension Service. 8 p

Moccaldi LA; Runkle ES (2007) Modeling the Effects of Temperature and Photosynthetic Daily Light Integral on Growth and Flowering of *Salvia splendens* and *Tagetes patula.* J. Amer Hort Soc 132:283-288. https://doi.org/10.21273/JASHS.132.3.283

Niu G, Heins RD, Cameron AC, Carlson WH (2001) Temperature and daily light integral influence plant quality and flower development of *Campanula carpatica* 'Blue Clips', 'Deep Blue Clips', and *Campanula* 'Birch Hybrid'. HortSci 36:664-668. https://doi.org/10.21273/HORTSCI.36.4.664

Nix HA (1976) Climate and crop productivity in Australia. *Climate and rice. IRRI, Los Baños, The Philippines*, 495-507.

Oh W, Cheon IH, Kim KS, Runkle ES (2009) Photosynthetic Daily Light Integral Influences Flowering Time and Crop Characteristics of *Cyclamen persicum*. HortSci 44:341-344. https://doi.org/10.21273/HORTSCI.44.2.341

Pallardy SG (2008) Physiology of Woody Plants, 3rd edition. Academic Press, New York.

Perry KB, Wehner TC, Johnson GL (1986) Comparison of 14 methods to determine heat unit requirements for cucumber harvest. HortSci 21:419-423.

Pramuk LA, Runkle ES (2005) Photosynthetic daily light integral during the seedling stage influences subsequent growth and flowering of *Celosia, Impatiens, Salvia, Tagetes,* and *Viola*. HortSci 40:1336-1339. https://doi.org/10.21273/HORTSCI.40.5.1336

Robertson GW (1968) A biometeorological time scale for a cereal crop involving day and night temperatures and photoperiod. Int J Biometeorol 12:191-223. https://doi.org/10.1007/BF01553422

Shirley HL (1929) The influence of light intensity and light quality upon the growth of plants. Amer Jour Bot 16:354-390. https://doi.org/10.1002/j.1537-2197.1929.tb09488.x

Simpson DG (1991) Growing density and container volume affect nursery and field growth of interior spruce seedlings. North J Appl For 8:160-165. https://doi.org/10.1093/njaf/8.4.160

Simpson DG (1994) Nursery growing density and container volume affect nursery and field growth of Douglas-fir and lodgepole pine seedlings. USDA forest service general technical report RM-257, pp. 104-114.

Sutton BC, Attree SM, El-Kassabi YA, Grossnikle SC, Polonenko DR (2004) Commercialization of somatic embryogenesis for plantation forestry. In: Walter C, Carson M (eds) Plantation forest biotechnology for the 21st century. Research Signpost pp. 275-301.

Sword-Sayer MAS, Brissette JC, Barnett JP (2005) Root growth and hydraulic conductivity of southern pine seedlings in response to soil temperature and water availability after planting. New For 30:253-272. https://doi.org/10.1007/s11056-005-7481-x

Sysoeva MI, Markovskaya EF (2006) PhotoThermal model of plant development. Rus J Plant Dev Biol 37:16-21. https://doi.org/10.1134/S1062360406010036

Teskey RO, Hinckley TM (1986) Moisture: effects of water stress on trees. In: Hennessey TC, Dougherty PM, Kossuth SV, Johnson JD (eds) Proceedings of the physiology working group technical session. SAF National Convention: Stress Physiology and Forest Productivity. Martinus Nijhoff Publishers, Dordrecht, The Netherlands, pp 9-33. https://doi.org/10.1007/978-94-009-4424-4_2

Teskey RO, Will RE (1999) Acclimation of loblolly pine seedlings to high temperatures. Tree Physiol 19:519-525. https://doi.org/10.1093/treephys/19.8.519

Teskey RO, Fites JA, Samuelson LJ, Bongarten BC (1986) Stomatal and nonstomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. Tree Physiol 2:131-142. https://doi.org/10.1093/treephys/2.1-2-3.131

Teskey RO, Bongarten B, Cregg, BM, Dougherty PM, Hennessey TC (1987) Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the characteristics of loblolly pine (*Pinus taeda* L.). Tree Physiol 3:41-61. https://doi.org/10.1093/treephys/3.1.41

Timmis R, Tanaka Y (1976) Effects of container density and plant water stress on growth and cold hardiness of Douglas-fir seedlings. For Sci 22:167-172.

Tschaplinski TJ, Blake TJ (1985) Effects of root restriction on growth correlations, water relations, and senescence of alder seedlings. Physiol Plant 64:167-176. https://doi.org/10.1111/j.1399-3054.1985.tb02331.x

Wang JY (1960) A Critique of the Heat Unit Approach to Plant Response Studies. Ecol 41:785-790. https://doi.org/10.2307/1931815

Will RE, Teskey RO (1997) Effect of elevated carbon dioxide concentration and root restriction on net photosynthesis, water relations and foliar carbohydrate status of loblolly pine seedlings. Tree Physiol 17:655-661. https://doi.org/10.1093/treephys/17.10.655