ORIGINAL PAPER

Individual variability and mortality required for constant final yield in simulated plant populations

Pavel Fibich · Jan Lepš · Jacob Weiner

Abstract When plant monocultures are sown over a wide range of densities for a given period of time, the total biomass yield increases with density at low densities and then levels off at high densities, a phenomenon called constant final yield (CFY). There are several reported cases, however, where the total yield decreases at very high densities, but the reasons for such exceptions are not known. We used a spatially explicit, individual-based "field of neighborhood" simulation model to investigate the potential roles of spatial pattern, individual variation, and competitive stress tolerance for CFY. In the model, individual plants compete asymmetrically for light when their fields overlap, and this competition decreases growth and increases mortality. We varied (1) the initial size variation, (2) the spatial pattern, and (3) ability to survive intense competition and examined the effects on the density-biomass relationship. CFY was always observed when there was high variability among individuals, but not always when variability was low. This high size variation could be the result of high initial size variability or variation in the degree of local crowding. For very different reasons, very high and very low tolerance for competition resulted in decreasing total biomass at very high densities. Our results emphasize the importance of individual variation for population processes and suggest that we should look for exceptions to CFY in homogeneous, even-aged, regularly spaced populations such as plantations.

Keywords Constant final yield · Variability · Mortality · Field of neighborhood · Simulation model

P. Fibich (✉) · J. Lepš
Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic
e-mail: pavel.fibich@prf.jcu.cz

J. Lepš
Institute of Entomology, Biology Center of the Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic

J. Weiner
Department of Plant and Environmental Sciences, University of Copenhagen, Rolighedsvej 21, DK-1958 Frederiksberg, Denmark

Introduction

If we grow plants of single species over a wide range of densities, we usually observe a linear increase in total biomass yield at low densities, which levels off at higher densities. This relationship is called "constant final yield" (CFY; Shinozaki and Kira 1956; Silvertown and Charlesworth 2001; Weiner and Freckleton 2010) or the asymptotic density-productivity relationship (Yahuza 2011; Willey and Heath 1969). CFY requires a density-dependent reduction in mean plant biomass and, at higher densities, density-dependent mortality (Bazzaz and Harper 1976). But it is theoretically possible that density effects can overcompensate for increasing density, such that total biomass production decreases at very high densities. This has been called a "parabolic" or unimodal density-productivity relationship (Yahuza 2011; Willey and Heath 1969), and it has been documented for some plant parts or yield components, such as fruit or seed production ("harvestable yield" in agronomy), e.g., grain yield of cereals (Willey and Heath 1969; Kristensen et al. 2008), and branch and leaf production in *Pinus densiflora* (Xue and Hagihara 2008).

With respect to total (usually above-ground only) biomass, density experiments with sufficiently high densities generally show CFY, but some exceptions have been documented (Farazdaghi and Harris 1968; Willey and Heath 1969; Wille, unpublished manuscript). We observed a unimodal

relationship of living biomass of *Agrostis capillaris* with the planting density (Stachová et al. 2013), but the relationship was consistent with CFY if dead as well as living biomass was included. Decrease of biomass at high densities has been reported for a clonal grass *Elymus nutans* (Chu et al. 2008) and for some crops, e.g., *Pisum sativum* (pea; Stoker 1975; Reynolds 1950), *Allium cepa* (onion; Bleasdale 1966; Rumpel and Felczynski 2000), *Glycine max* (soybean; Rahman and Hossain 2011), *Daucus carota* (carrot; Li et al. 1996), and *Lactuca sativa* (lettuce; Scaife and Jones 1976), and for one of nine comparisons of *Arabidopsis thaliana* (Stoll et al. 2002). Scaife and Jones (1976) reported a slight decrease in total yield at sowing density over 17,000 seed per m^2, but even higher densities have been reported from nature, more than 10^3 seedlings per 0.01 m^2 for some species (Prach 1982). CFY has been documented in some studies that included very high sowing densities (Kays and Harper 1974). The generality of CFY has not yet been definitively established (W. Wille, unpublished manuscript).

Variability in size of individuals has major effects on population dynamics (Uchmanski 2000). We hypothesize that variability is necessary for CFY, and therefore factors increasing size variability will promote CFY. Self-thinning is necessary for CFY at very high densities (Weiner and Freckleton 2010), and self-thinning is preceded by very high size inequality, after which the smallest individuals die, and the size variation among survivors decreases (Weiner and Thomas 1986). In theory, if competition is completely size asymmetric, it always results in CFY (Pacala and Weiner 1991). If competition is not size asymmetric, less size variation develops and the smaller plants do not die (Yastrebov 1996), or they die at a much slower rate (Stoll et al. 2002). In this latter case, growth of the whole stand slows down, larger individuals, which contribute most to the total biomass, grow more slowly than they would if there were mortality of the smaller individuals. Thus, without size-asymmetric competition and resultant size variation, very high densities may produce less biomass than somewhat lower densities.

Similarly, if all the individuals are initially of similar size, less variation in size will develop. Spatial pattern can also contribute to size variation in the plant populations (Miller and Weiner 1989; Bonan 1991; Hara and Wyszomirski 1994; Weiner et al. 2001), because a high degree of spatial aggregation means a high degree of variation in local crowding. Spatial heterogeneity in environmental conditions will also increase size variability (Chu et al. 2009). Species differ in their tolerance to competition; some respond by decreasing growth or by increased mortality. Stress tolerators usually decrease their growth but are able to survive for a long time, whereas for fast-growing species, a reduction in an individual's grow rate is often followed by death. If individuals die quickly due to competition, this provides space and resources for the others, increasing total biomass production.

Here, we present a theoretical study using a spatially explicit, individual-based model (Grimm and Railsback 2005) "field of neighborhood" model of plant growth and competition (Berger and Hildenbrandt 2000), in which the effect of competition decreases with distance between individuals, and allometric growth is influenced by neighborhood competition (Fibich and Lepš 2011). We investigate the role of spatial pattern, variability of individuals, and competitive stress tolerance for CFY and ask what theoretical conditions are necessary for CFY. Specifically, we want to test the effect of (1) initial variability (e.g., due to variability in germination time, seed size, and initial growth rates), (2) the initial spatial pattern of individuals, and (3) competitive stress tolerance, defined as the length of time individuals survive intense competition before dying.

Methods

Model design, state variables, and initialization

We use an individual-based model for growth and competition (Fibich and Lepš 2011) of an even-aged stand of plants. Each plant grows in discrete time steps and has position in continuous space modeled as a torus with 100×100 arbitrary units. Each individual plant has parameters for initial biomass, maximum potential biomass, height-radius ratio, growth rate, shade tolerance (efficiency of usage of light for growth in one time step), competitive tolerance (length of time it can survive under strong competition), and three field of neighborhood (FON) parameters, which represent size and shape of FON (Berger and Hildenbrandt 2000).

At the beginning of a simulation, we generated individual plant parameters (Table 1) from a lognormal distribution using log-transformed means and standard deviations (SD) of parameters. A factorial design is used with 47 initial densities and three spatial pattern types. In the regular pattern, individuals are located in a regular square grid, one individual in one grid cell. These positions of individuals in the grid cell are randomized by moving azimuths distances around the center of grid cell randomly, but not further than the half of size of grid cell. Size of the grid cell is the reciprocal of the square root of plant density. The regular grid is used only for the regular spatial pattern. Random positions of homogeneous Poisson process were used to generate the random spatial pattern. In the clumped pattern, the locations of clump centers are generated randomly. At the clump center, the individual has the highest probability to establish, and the probability decreases with distance from the center (it simulates homogeneous Gauss-Poisson cluster process, see Lepš and Kindlmann 1987). There are always 16 clumps of the same size.

Table 1 Plant parameters and variables with mean values and standard deviations (SD) for log-normal distribution

Plant parameter	Value	
Initial height-radius ration (v)[a]	2	
Minimum at FON border (f^{min})[b]	0.1	
R_a – FON parameter[b]	3	
R_b – FON parameter[b]	0.6	
Plant variables	Mean value	SD (log scale)
Initial biomass (b^{ini})[a]	2	0.01 (0.4 in the scenario C)
Maximum biomass (b^{max})[a]	100	0.01
Growth rate (g)	0.05	0.001
Shade tolerance (s)[b]	1.5	0.01
Competitive stress tolerance(l)[a]	30 (8 in the scenario B)	0.15

SD values are in the log scale. If it is not written otherwise, values of parameters are not changed or belong to the scenario A

[a] Taken from Fibich and Lepš (2011)

[b] Taken from Berger and Hildenbrandt (2000) and Berger et al. (2004)

Growth

We designed plants as cones with biomass corresponding to cone volume (Fibich and Lepš 2011). The plant biomass b growth follows a logistic growth curve with sigmoidal shape, and it is reduced by competition C (The value of C is equal to 1 when there is no competition, and C decreases with increasing competitive effects of neighbors).

$$\mathrm{d}b/\mathrm{d}t = bg(1-b/b^{max})C \qquad (1)$$

Each plant has radius r, height h, and defined an initial height-radius ratio v. After each step, new values for height $h+x$ and radius $r+y$ are calculated. The values x and y are calculated as height-radius ratio divided by competitive reduction (C) so that the cone volume corresponds to the plant new biomass b. Initial height-radius ratio v is used for increase of height and radius dimensions if the plant is not under competition ($C=1$); in this case, the plant keeps its original shape. Height growth is preferred under strong competition (small C): the plant then increases its investment into height rather than radius growth. This corresponds to plasticity or shade avoidance due to competition in real populations (Weiner and Thomas 1992). Neither radius nor height of a living plant can decrease. Height is used for determining the asymmetric competition for light (taller plants are less shaded by smaller neighbors than vice versa). Initial height and radius are computed from generated initial biomass (volume of cone) and height-radius ratio (v). This ratio, together with the maximum biomass (b^{max}), determines a maximum height of plant (e.g., with $b=b^{max}\sim100$, $v=h/r=2/1$ and no competition, we get from $100=h\pi r^2/3$ the maximum height 7.258). After reaching the maximum height, plant can grow only in radius.

Competition

We assumed competition for light only. The FON approach considers a field with circular base around each plant and intensity of field is decreasing with increasing distance from plant (Berger and Hildenbrandt 2000). Overlapping fields of different plants reflect competition for light among these plants. The circular base of FON (B) is a function of plant radius r, $B=R_a r^{Rb}$ where R_a and R_b are FON parameters (Table 1; Berger and Hildenbrandt 2000). Competition for light is expressed by $C=\max\{0, 1-F/s\}$ where s is shade tolerance of plant and F is strength of the neighborhood (Berger et al. 2006). F is high if competition (shading) by neighbors is strong. A plant with high shade tolerance s is able to survive and grow even if it is shaded by neighboring plants. The neighborhood strength F of plant k is expressed by sum of competition strengths of all the neighboring plants $F = 1/A \sum_{n \neq k} N(\mathrm{k},n)$ where A is the area of the zone of influence (ZOI) of the focal plant, and B is its radius (Berger and Hildenbrandt 2000). $N(k, n)$ defines strength of competition for plant k caused by plant n. It scales a FON according to differences in the height of competing plants k and n (Fibich and Lepš 2011). If the plant k is higher than the plant n, then plant k is affected less by competition from n than plant n from plant k. FON exponentially decreases from 1 at the radius of a plant to the plant-specific small value f^{min} at the border of the ZOI; it is 0 outside of the ZOI (Berger and Hildenbrandt 2000). Therefore, a near neighbor influences a plant more than a distant neighbor.

Mortality

Mortality is caused only by competition. The death of a plant k depends on the sum of competition values (C) over last l_k time steps (t). Plant k dies if

$$\sum_{t=\mathrm{now}-l_k}^{\mathrm{now}} C_{k,t} < 0.05. \qquad (2)$$

C decreases with increasing competition, so that it might be considered as proportion of resources a plant is able to enquire (comparing to 1 without competition) during a time step. In our model, the plant dies if it is not able to enquire in last l

steps at least 0.05 of the amount it would enquire in one time step without competition. Consequently, the higher is the l value, the longer the plant is able to survive under intense competition: it characterizes the tolerance to competition stress with respect to survival but does not affect the sensitivity of growth to competition. Thus, a plant can survive competition instead of dying immediately after the strength of competition reaches a threshold. It reflects the speed with which a plant dies when suffering from very strong competition (i.e., high value of l denotes an ability to tolerate competition and therefore slow speed of mortality). We call parameter l competitive stress tolerance, implying that tolerators are able to survive even when their growth is decreased. At the beginning, all $C_{k,t<0}$ are set to 1. After a plant's death, actual height-radius ratio is saved (to retain the ratio after biomass changes) and biomass is decreased by 1/3 at each time step. It reflects the fact that biomass of a dead plant also shades its neighbors to some degree for a period of time.

Scenarios

We varied systematically values of the three parameters that we hypothesize to be important for CFY: the initial variability, spatial pattern, and the ability to survive strong competition, and for each parameter combination, we calculated a simple measure characterizing whether the results are consistent with CFY (see below). Based on these results, we selected three scenarios with rather extreme values for competitive stress tolerance and the initial biomass variability (Table 1) and inspected their behavior in much detail. Scenario A is a baseline with the low variability of initial biomass and high competitive stress tolerance (high value of parameter l). Scenario B had lower competitive stress tolerance (lower value of l) than scenario A, while scenario C had higher variability of initial biomass (higher SD) than scenario A.

Our results are based on 101 runs of simulations of 150 discrete steps each. The number of time steps is based on the growth rate necessary to achieve an individual's maximum biomass (Table 1). Mean coefficients of variation (CV) (= standard deviation/mean) of individual biomass (for each replication was computed one CV value, and the values were averaged over all the replications) characterizes the size variability of individuals. CV values were multiplied by 100 to express them as percent.

Characterization of CFY

The population follows CFY if its yield increases monotonically and then levels off with increasing density (Weiner and Freckleton 2010). To evaluate if the replicated population follows CFY, we used the ratio of the mean yield at the highest density to the mean yield of the density giving the highest yield. Because the model is stochastic, the values of individual runs vary. If the ratio is equal or close to 1 (it covers the situations that yield is increasing or levels off along the entire density gradient), then population is considered to follow CFY. Low ratio values are considered evidence of behavior not consistent with CFY.

Results

Variability in initial biomass, competitive stress tolerance (parameter l), and the spatial pattern all had considerable effects on the relationship between density and total biomass. For all the spatial patterns, very low competitive stress tolerance resulted in behavior not consistent with CFY (Fig. 1). CFY was observed in the clumped pattern under the widest range of parameter values, and in regular pattern under the narrowest range. In all the spatial patterns, increase in initial variability of individuals promoted CFY, whereas the competitive stress tolerance showed CFY at intermediate values (Fig. 1).

Mean biomass of surviving plants increased over time and was the highest in the clumped pattern (Fig. 1 in the Supplementary Materials). The highest mean biomass and lowest variability of individual biomass was observed in scenario B (the lowest competitive stress tolerance), compared to other two scenarios. The decrease in the number of surviving plants was fastest and reached the lowest values in scenario B (Fig. 2, Supplementary Materials). The clumped pattern had the lowest proportion of surviving plants.

Scenario A. Low initial variability and high competitive stress tolerance

Simulated populations in a clumped pattern always showed a behavior consistent with CFY, but the other two patterns did not (Fig. 2). The clumped pattern generally had the lowest total yield and the lowest number of surviving plants compared to the other patterns. Mean plant biomass decreased and the number of surviving plants increased with increasing density for all spatial patterns. In the clumped pattern, there was higher mean plant biomass at the high density than in the other patterns (Fig. 2b). The clumped pattern had the highest variability in individual biomass, whereas the variability in the other two patterns was lower, resulting in more equal competition. This, together with long survival under competition, resulted in many small surviving individuals in regular and random patterns. At the highest density, the frequency of large individuals is clearly highest in the clumped pattern (Fig. 3 in the Supplementary Materials).

Scenario B. Low competitive stress tolerance

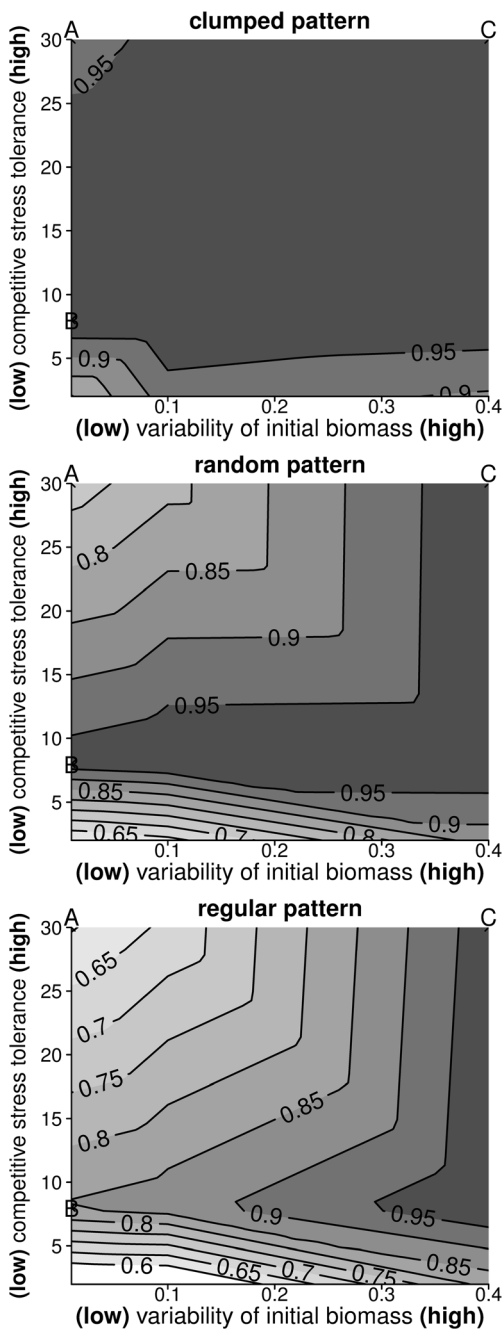When plants do not tolerate intense competition (Table 1), the clumped and random patterns showed CFY, but regular

Fig. 1 Dependence of the ratio between the mean yield at the highest density and the highest yield at any density on the variability of initial biomass and competitive stress tolerance. A, B, and C denote positions of the presented scenarios in the parameter space. *Darker color* means situation closer to CFY

Fig. 2 Total biomass (**a**), mean biomass of plant (**b**), and number of surviving plants (**c**) and their coefficients of variation (CV; *lines*) versus initial density for the clumped, regular, and random spatial pattern in the scenario A. CV in **b** describes the variability among individuals

pattern did not (Fig. 3a). After decrease of mean biomass and increase of number of survivors up to a density of around 1,300 individuals, the different patterns behaved very differently (Fig. 3b, c). The regular pattern showed the most extreme values of biomass and number of survivors. For all spatial patterns, the total and mean biomass values were higher and number of surviving individuals lower than in
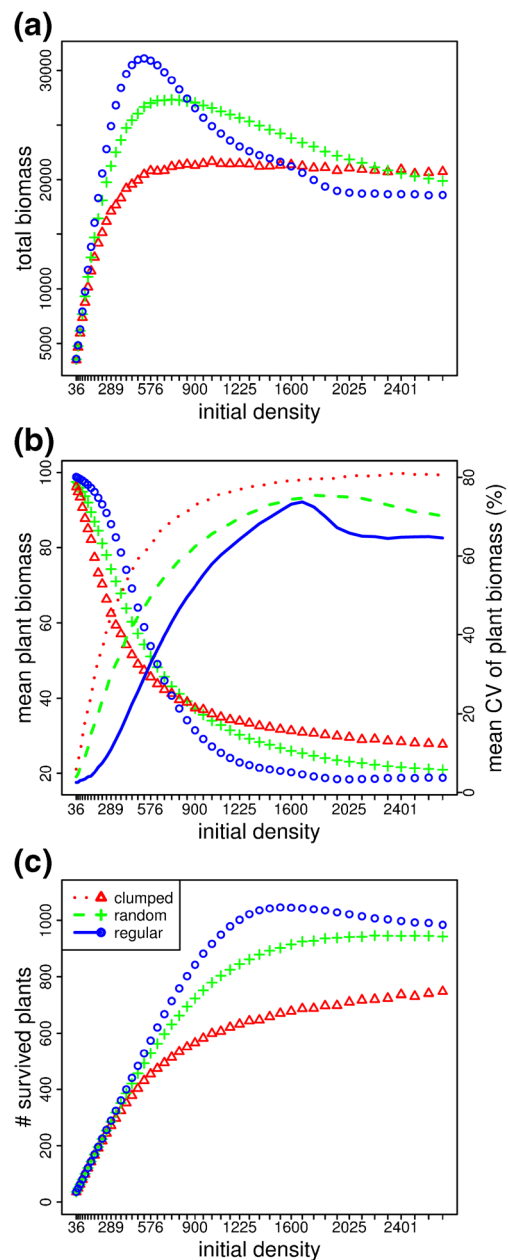
scenario A (Figs. 2 and 3). Distribution of biomass, height, and radius were similar for all spatial patterns, but there were more individuals with the highest biomass, height, and radius than in the scenario A (Figs. 3 and 4 in the Supplementary Materials). Lower competitive stress tolerance allowed the faster growth of survivors, and therefore differentiation among individuals, although there was lower variability of individual biomass compared to scenario A (Fig. 1 in the Supplementary Materials). At the high densities in the regular pattern, the number of surviving
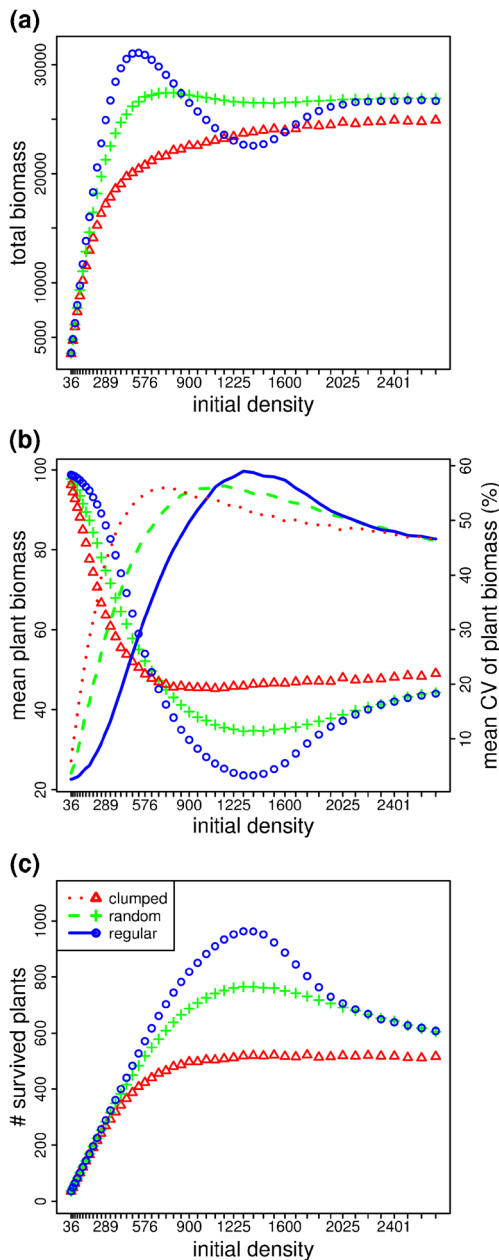
Fig. 3 Total biomass (**a**), mean biomass of plant (**b**), and number of survived plants (**c**) and their coefficients of variation (CV; *lines*) versus initial density for the clumped, regular, and random spatial pattern in scenario B. CV in **b** describes the variability among individuals

Fig. 4 Total biomass (**a**), mean biomass of plant (**b**), and number of survived plants (**c**) and their coefficients of variation (CV; *lines*) based on initial density for the clumped, regular, and random spatial pattern in the scenario C. CV in **b** describes the variability between individuals

individuals decreased from a maximum of 900 to 600 individuals in the highest density.

Scenario C. High initial variability

When initial variability in biomass was high (Table 1), all spatial patterns produced results consistent with CFY (Fig. 4a). Mean biomass and number of surviving plants showed similar trends as in the scenario A, decreasing with increasing density, but at the highest densities, the number of individuals who survived and mean biomass were higher in
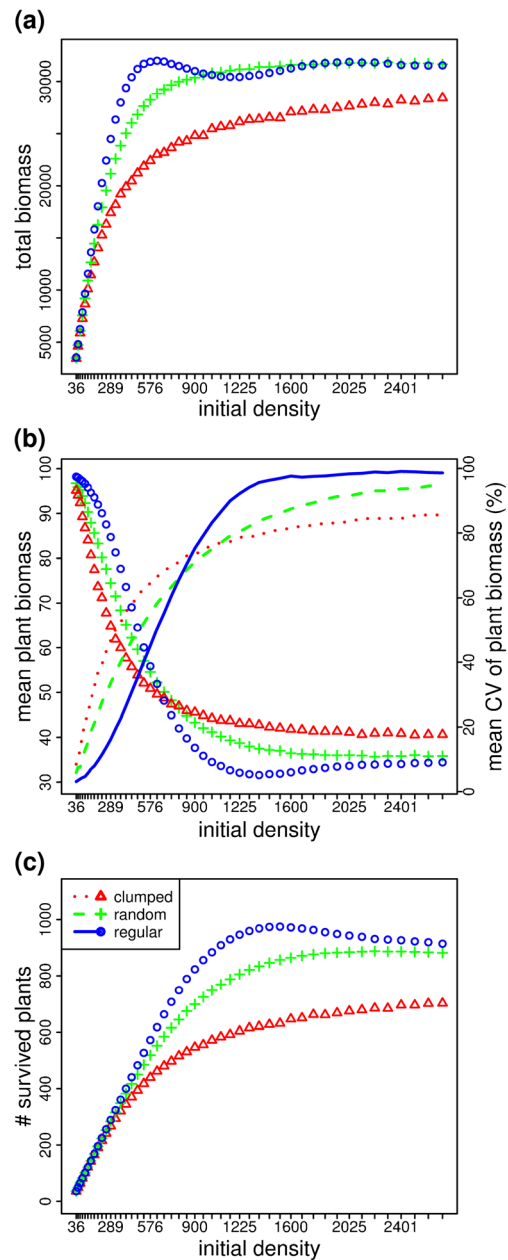
this scenario than in scenario A (Figs. 2b, c and 4b, c). The regular and random patterns also showed higher variability in biomass than in scenario A and than the clumped pattern at densities higher than 800 individuals (Figs. 3b and 4b). Distributions of biomass, height and radius were bimodal and similar for all spatial patterns (Fig. 5, Supplementary Materials). But there were more individuals with the highest biomass, height, and radius in Scenario C than in the scenario A (Figs. 3 and 5 in the Supplementary Materials) and CFY was observed.

Discussion

In our simulations, the initial variability, the spatial pattern, and competitive stress tolerance all have implications for CFY.

Size variation and CFY

Variability among plants is amplified by size-asymmetric competition (Weiner et al. 2001). In populations with much size variability, the largest individuals are not affected much by asymmetric competition, even at very high densities, and the final total yield does not decrease at high densities. Small size differences mean that plants of similar sizes suffer similarly from competition, which leads to many equally small plants. If self-thinning occurs slowly due to high competitive stress tolerance, the population is composed by many small individuals, which together have lower biomass than fewer larger individuals filling the same area would have (Yoda et al. 1963). Theoretically, if there is no variability (and so the competition is completely symmetric), and plants are in perfect regular patterns (so that the distances to the competing neighbors are exactly the same), at some point, all plants would be below the threshold for survival and all will stop growing or die at the same time. It has been shown that extremely asymmetric competition always produces CFY, irrespective of the competition model (Pacala and Weiner 1991). Similarly, our results suggest that if the initial variability exceeds a threshold, which increases the effects of asymmetric competition, the system produces CFY under a wide range of other parameters. A clumped spatial pattern is one potential source of variability in competition among individuals, because plants at the centers of clumps experience stronger competition than plants at the borders. It has been demonstrated that a nonuniform pattern of individuals can mimic the effect of asymmetric competition (Miller and Weiner 1989; Bonan 1991; Weiner et al. 2001). Consequently, the clumped pattern promotes CFY even under the parameter values that do not result in CFY in the regular and random patterns. Not surprisingly, the variability of individual biomass was the highest in the clumped pattern, as in previous studies (Hara and Wyszomirski 1994; Weiner et al. 1998; Weiner et al. 2001).

Relevant empirical results

Agricultural studies on the sowing density effect are usually consistent with CFY, but very high densities are not usually investigated. The deviations from CFY were observed in some row crops, grown in regular patterns, e.g., *A. cepa* (Bleasdale 1966; Rumpel and Felczynski 2000), *L. sativa* (Scaife and Jones 1976), and *G. max* (Rahman and Hossain 2011). Decreases in root and total biomass of *D. carota* at the high densities have been reported (Li et al. 1996), although

shoot biomass did not show this. Total population biomass of clonal grass *E. nutans* was highest at intermediate densities (Chu et al. 2008), although this was attributed to facilitation at intermediate densities in an extreme environment. A decrease in living biomass at high densities was observed in the grass *A. capillaris* (Stachová et al. 2013), although this was accompanied by a corresponding increase in dead biomass at the highest density. An increase of productivity with a reduction of stand density was observed in forest plantations of *Picea abies* and *Fagus sylvatica* (Pretzsch 2003). Overcompensating negative density dependence was also observed for the recruits of tropical tree *Plerandenophora longicuspis*, where fungal pathogens caused 90–100 % mortality at the high densities (Bagchi et al. 2010).

Our results show more deviations from CFY than reported from experimental studies. One of the reasons may be that experimental studies usually have more initial size variation than our model, because individuals in the field germinate over a period of time (Kotorova and Leps 1999), and because of spatial heterogeneity.

Variability of initial biomass is amplified during stand development by asymmetric competition, which promotes CFY in all spatial patterns. This leads to higher mortality, but also higher mean plant biomass. As in previous studies (Stoll et al. 2002; Symonides 1983a, 1983b; Taylor and Aarssen 1989; Weiner et al. 2001), final variability in individual biomass generally increased with density in our model.

The ability to survive strong competition

If the effect of competition exceeds the level a plant can tolerate, plant's growth slows down or stops, and then it dies. Plant species differ in their sensitivity of their growth and survival to competition. Our competitive stress tolerance parameter (l) characterized the time that a species is able to survive under strong competition. A long competitive stress tolerance period allows plants to survive even with highly reduced growth. If plants survive for longer time under competition stress in populations without a strong size hierarchy, then growth of all the individuals is reduced and total productivity is low. If plants survive under competition stress only for a short time, then mortality will occur faster, resulting in more space for the survivors and a faster development of the stand. When competitive stress tolerance was very low, the number of individuals drops quickly, faster than can be compensated by the subsequent growth of survivors. This represents a theoretical extreme case, which might not occur in nature, because the real populations are never as synchronized as in our model. Considering the biology of species with reported deviations from CFY (Bleasdale 1966; Stoker 1975; Li et al. 1996; Rahman and Hossain 2011), our results suggest that these deviations are due to decreased growth and low mortality in response to competition, not fast mortality.

CFY resulted more often in the clumped and random patterns, than in the regular pattern. The regular pattern is the most extreme of all spatial patterns, because similarity in plant size is reinforced by spatial uniformity: all plants have the same neighborhood. Mortality in the regular pattern was very strong when it occurred, reducing the number of surviving individuals and producing the lowest mean biomass. Not surprisingly, variability of individual biomass was the lowest for the regular pattern (Weiner et al. 2001).

Our model results emphasize the importance of variability among individuals for CFY. In our model, high variability resulted from initial variability or by variability in competition caused by variability in local crowding (this variability increases from regular to clumped pattern). The size inequality causes mortality of subordinate individuals, which is necessary for CFY at high densities (Weiner and Freckleton 2010). Thus, the deviations from CFY are most likely under very high densities when similarly sized individuals are planted in regular pattern (planted rather than sown, as seedling establishment is affected in many small-scale factors and often results in size inequality). Similarly sized individuals then experience similar level of competition, and the population of many small individuals has low total yield. This is more likely, if plants react to competition by slowing of their growth, but are able to survive for a long time as small, suppressed individuals.

References

Bagchi R, Swinfield T, Gallery RE, Lewis OT, Gipenger S, Narayan L, Freckleton RP (2010) Testing the Janzen-Connell mechanism: pathogens causes overcompensating density dependence in the a tropical tree. Ecol Lett 13:1262–1269

Bazzaz FA, Harper JL (1976) Relationship between plant weight and numbers in mixed populations of *Sinapis alba* (L.) Rabenh. and *Lepidium sativum* L. J Appl Ecol 13:211–216

Berger U, Hildenbrandt H (2000) A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecol Model 132:287–302

Berger U, Hildenbrandt H, Grimm V (2004) Age-related decline in forest production: modelling the effects of growth limitation, neighbourhood competition and self-thinning. J Ecol 92:846–853

Berger U, Adams M, Grimm V, Hildenbrandt H (2006) Modelling secondary succession of neotropical mangroves: causes and consequences of growth reduction in pioneer species. Perspect Plant Ecol Evol Syst 7:243–252

Bleasdale JKA (1966) The effects of plant spacing on the yield of bulb onion (*Allium cepa* L.) grown from seed. J Hortic Sci 41:145–153

Bonan GB (1991) Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. Ann Bot 68:341–347

Chu CJ, Maestre FT, Xiao S, Weiner J, Wang YS, Duan ZH, Wang G (2008) Biomass-density relationships in plant populations are determined by the balance between facilitation and resource competition. Ecol Lett 11:1189–1197

Chu CJ, Weiner J, Maestre FT, Xiao S, Wang YS, Li Q, Yuan JL, Zhao LQ, Ren ZW, Wang G (2009) Positive interactions can increase size inequality in plant populations. J Ecol 97:1401–1407

Farazdaghi H, Harris PM (1968) Plant competition and crop yield. Nature 217:289–290

Fibich P, Lepš J (2011) Do biodiversity indices behave as expected from traits of constituent species in simulated scenarios? Ecol Model 222:2049–2058

Grimm V, Railsback SF (2005) Individual-based modeling and ecology. University Press, Princeton

Hara T, Wyszomirski T (1994) Competition asymmetry reduces spatial effects on size-structure dynamics in plant populations. Ann Bot 73:285–297

Kays S, Harper JL (1974) The regulation of plant and tiller density in a grass sward. J Ecol 62:97–105

Kotorova I, Leps J (1999) Comparative ecology of seedling recruitment in an oligotrophic wet meadow. J Veg Sci 10:175–186

Kristensen L, Olsen J, Weiner J (2008) Crop density, sowing pattern and nitrogen fertilization effects on weed suppression and yield in spring wheat. Weed Sci 56:97–102

Lepš J, Kindlmann P (1987) Models of development of spatial pattern of an even-aged plant population over time. Ecol Model 39:45–89

Li B, Watkinson AR, Hara T (1996) Dynamics of competition in populations of carrot (*Daucus carota*). Ann Bot 78:203–214

Miller TE, Weiner J (1989) Local density variation may mimic effects of asymmetric competition on plant size variability. Ecology 70:1188–1191

Pacala SA, Weiner J (1991) Effects of including competitive asymmetry in a local density model of plant interference. J Theor Biol 149:165–179

Prach K (1982) Self-thinning processes in selected ruderal species populations. Preslia 54:271–275

Pretzsch H (2003) The elasticity of growth in pure and mixed stands of Norway spruce (*Picea abies* L. Karst.) and common beech (*Fagus sylvatica* L.). J For Sci 49:491–501

Rahman MM, Hossain MM (2011) Plant density effects on growth, yield and yield components of two soybean varieties under equidistant planting arrangement. Asian J Plant Sci 10:278–286

Reynolds JD (1950) Spacing trials with dried peas. Agriculture 56:527–537

Rumpel J, Felczynski K (2000) Effect of plant density on yield and bulb size of direct sown onions. Acta Horticult 533:179–186

Scaife MA, Jones D (1976) The relationship between crop yield (or mean plant weight) of lettuce and plant density, length of growing period, and initial plant weight. J Agric Sci 86:83–91

Shinozaki K, Kira T (1956) Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. J Inst Polytechnics Osaka City Univ 7:35–72

Silvertown J, Charlesworth D (2001) Introduction to plant population biology. Blackwell, London

Stachová T, Fibich P, Lepš J (2013) Plant density affects measures of biodiversity effects. J Plant Ecol 6:1–11

Stoker R (1975) Effect of plant population on yield garden peas under different moisture regimes. N Z J Exp Agric 3:333–337

Stoll P, Weiner J, Muller-Landau H, Müller E, Hara T (2002) Size symmetry of competition alters biomass-density relations. Proc R Soc B 296:2191–2195

Symonides E (1983a) Population size regulation as a result of intra-population interactions 1. Effect of density on the survival and development of individuals of *Erophila verna* (L.). Ekologia Polska 31:839-882

Symonides E (1983b) Population size regulation as a result of intra-population interactions 2. Effect of density on the growth rate morphological diversity and fecundity of *Erophila verna* (L.). Ekologia Polska 31:883-912

Taylor DR, Aarssen LW (1989) On the density dependence of replacement-series competition experiments. J Ecol 4:975–988

Uchmanski J (2000) Individual variability and population regulation: an individual-based model. Oikos 90:539–548

Weiner J, Freckleton R (2010) Constant final yield. Annu Rev Ecol Evol Syst 41:173–192

Weiner J, Thomas SC (1986) Size variability and competition in plant monocultures. Oikos 47:211–222

Weiner J, Thomas SC (1992) Competition and allometry in three species of annual plants. Ecology 73:648–656

Weiner J, Kinsman S, Williams S (1998) Modeling the growth of individuals in plant populations: local density variation in a strand population of *Xanthium strumarium*. Am J Bot 85:1638–1645

Weiner J, Stoll P, Muller-Landau H, Jasentuliyana A (2001) The effects of density, spatial pattern and competitive symmetry on size variation in simulated plant populations. Am Nat 158:438–450

Willey RW, Heath SB (1969) The quantitative relationships between plant population and crop yield. Adv Agron 24:281–322

Xue L, Hagihara A (2008) Density effects on organs in self-thinning *Pinus densiflora* Sieb. Et Zucc. stands. Ecol Res 23:689–695

Yahuza I (2011) Yield-density equations and their application for agronomic research: a review. Int J Biosci 1:1–17

Yastrebov AB (1996) Different types of heterogeneity and plant competition in monospecific stands. Oikos 75:89–97

Yoda K, Kira T, Ogawa H, Hozumi K (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. J Biol Osaka City Univ 14:107–129