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Yield–density relationships of above- and belowground organs in *Allium cepa* var. *aggregatum* populations

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Abstract The quantitative response of yield to density in plant populations has been an important focus of both theoretical research and empirical research. Most studies on yield–density effects have focused mainly on aboveground plant parts, and rarely on various plant organs and belowground parts. We tested the hypothesis that yield-density effects of belowground parts are different from those for aboveground parts. Bulbs of *Allium cepa* var. *aggregatum* were sown at five densities at the Pasture Ecology Research Station, western Jilin Province, China. We harvested populations at four different points in time and analyzed yield–density relationships of above- versus belowground parts and component organs. A hyperbolic model provided a very good fit to above- and belowground biomass, as well as the biomass of specific organs throughout the experiment. Aboveground and leaf biomass achieved constant final yield, but stand stem and root biomass increased monotonically with increasing sowing density. Belowground and specifically bulb yield was highest at intermediate densities at the later harvests. Constant final yield may be widely applicable to total biomass production by a population, but it does not apply to specific organs, such as stems, roots, or bulbs. Asymptotic leaf biomass reached its asymptote earlier than that of other aboveground parts. The effect of density on *A. cepa* var. *aggregatum* organs is a consequence of allocation of photosynthate to different organs in response to competition. Yield–density effects are different above- and belowground as a result of the different mechanisms of competition,

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constrained by the functional relationship between above- and belowground organs.

Keywords Aboveground competition · Belowground competition · Constant final yield · Density effect · Optimum density · Plant organ

Introduction

The yield–density relationship is central to quantitative and theoretical ecology (Vandermeer 1984). One of the most well-established patterns of yield–density relationships within monocultures is constant final yield (CFY; Weiner and Freckleton 2010) or the asymptotic density–productivity relationship (Yahuza 2011). If plant monocultures are sown over a wide range of densities for a given period, we usually observe a linear increase in total standing biomass at low densities, which levels out as densities increase further (Shinozaki and Kira 1956; Fibich et al. 2014). Size-asymmetric competition and plasticity in allometric growth are usually the mechanisms invoked to explain this pattern, and it also has a clear evolutionary basis (Weiner and Freckleton 2010). Despite evidence that CFY is quite general, several exceptions (unimodal or "parabolic" density–productivity relationships) have been reported for some row crops, e.g., *Lactuca sativa* (lettuce; Scaife and Jones 1976) and *Glycine max* (soybean; Rahman et al. 2011). Overcompensating negative density dependence was observed in a tropical tree *Pleradenophora longicuspis* (Bagchi et al. 2010), and a clonal grass *Elymus nutans* (Chu et al. 2008) grown at different densities on the Tibetan Plateau. A decline of total biomass production with an increase of stand density was also observed in plantations of *Fagus sylvatica* and *Picea abies* (Pretzsch 2003).

Most studies on yield–density effect have focused only to aboveground parts—there have been fewer studies on specific organs and even fewer on belowground parts (Shinozaki and Kira 1956; Vandermeer 1984; Stachová et al. 2013). Allocation to different organs changes over the course of development and is sometimes plastic. For example, leaves are shed as new ones grow at the top, compared to annual increments in stems (Deshar et al. 2012). As a result, yield–density relationships for stems and leaves might be expected to be fundamentally different. Exploring the density effects on different plant organs is necessary for population density management in relation to population yield estimation.

A unimodal density–biomass relationship has been documented for some plant parts or yield components. A decrease in seed or grain yield at very high densities has been reported for forages and cereals (Donald 1951; Kristensen et al. 2008). The woody plant *Pinus densiflora* showed decreased branch and leaf biomass at high densities (Xue and Hagihara 2008). Despite the progress made so far, few studies have investigated yield–density effects for both above- and belowground organs.

The processes and mechanisms of plant competition differ fundamentally between above- and belowground (Cahill 1999). Plants compete primarily for light above ground and for mineral nutrients and water below ground. The resources are fundamentally different, which makes the mechanisms of competition for them also very different (Casper and Jackson 1997). The spatial division between shoots and roots and the different microenvironments they experience increase the mechanistic differences between above- and belowground competition processes (McPhee and Aarssen 2001). One fundamental mechanistic difference is that aboveground competition is size asymmetric, whereas belowground competition is usually size symmetric (Weiner et al. 1997). This could result in different yield–density relationships for above- and belowground parts. A study conducted with *Daucus carota* (carrot) showed that yield–density relationships were different above- and belowground (Li et al. 1996). Although belowground parts are as important for plants as those above ground (Trumbore and Gaudinski 2003), belowground density effects have received relatively little attention, and there have been very few comparisons between above- and belowground yield–density relationships.

In this study, we address the following questions: (i) Is CFY observed in *A. cepa* var. *aggregatum*? (ii) Are yield–density relationships for aboveground and belowground parts different? (iii) What differences exist among yield–density relationships of different organs (leaves, stems, bulbs, and roots)? These questions were investigated experimentally by growing *A. cepa* var. *aggregatum* populations over a wide range of densities.

Materials and methods

Study species

Onion is by far the most important bulb plant cultivated throughout the world. A large variety of onion cultivars and land races have been developed over centuries to fit diverse climates and food preferences of different regions and cultures. *Allium cepa* var. *aggregatum* (Liliaceous), called tillered onion, shallot, potato onion, is a perennial herb native to Central and Western Asia. This species is grown as an annual and is an important vegetable worldwide because of its rich nutrients, medicinal and culinary value, and high yield. It is widely cultivated in the northeast area of China, especially Heilongjiang and Jilin Provinces. Although the yield of tillered onion is somewhat less than that of garden onion (*A. cepa* L.), it is characterized by strong tillering, stress tolerance, fast growth, and short growing period. It does not suffer from diseases or pests as much as most crops and can enhance the cropping index and reduce pesticide use. Consequently, tillered onion can serve as an alternative crop in areas and seasons that are not suitable for the cultivation of garden onion.

Tillered onion is well known and commonly used as experimental material due to its low cost, short test time, ease of cultivation and storage, large number of roots, and well-developed belowground parts, which made it a very suitable material for the present study. Individual plants can form multiple small spherical bulbs. Tillered onion has tube-like leaves, approximately 30 cm in length, but narrower than those of garden onion. The plant rarely flowers or sets seeds due to the long time artificial selection, and is propagated as small bulbs for crop production. The most common plant spacing in agricultural stands of tillered onion in the Northeastern China is 13–15 cm.

Experimental design

The experiment was conducted at the Pasture Ecology Research Station of Northeast Normal University, Changling, Jilin Province, China (123°44′E, 44°40′N) in 2008. Healthy, intact, and equal-sized onion bulbs of A. *cepa* var. *aggregatum* (average diameter, 5 cm, mean fresh weight, 34.9 g) without any fresh roots and leaves were purchased from local market in Changchun, Jilin Province, China. Bulbs were stored dry at 4 °C and returned to room temperature (20–22 °C) before sowing.

The experiment was a completely randomized block design with five sowing densities, three replicate blocks, and four harvests. To investigate a wide range of densities, bulbs were sown in the field in a grid pattern at inter-plant spacings of 19, 16, 13, 10, and 7 cm (36, 49, 64, 121, and 225 ind. m^{-2}), to which we refer below as very low (LL), low (L), medium (M), high (H), or very high (HH) density. Holes were punched into the soil to a depth of 6 cm, and one bulb was placed in each hole, which was subsequently covered with soil. Sowing was performed on 7 May. Individual plots were 5 m × 5 m, with 20 columns and 20 rows, and were surrounded by 3 guard rows. Fertilizer (15 % N, 15 % P, 15 % K, Yuntianhua Agricultural Development Co., LTD, Changchun) was supplied to all plots before sowing at the recommended rate of 133 g m^{-2}. Plots were irrigated periodically and sprayed with Phoxim (Lisheng Agricultural Science and Technology Co., LTD, Changchun) against maggots on 8 June. No additional nutrients were supplied during the growing season.

Samples were harvested 17, 33, 49, and 65 days after sowing. At the final samplings, leaves of plants were nearing senescence, but there was no sign of bolting. At each harvest and for each density, 30 plants, 10 from each block, were randomly selected and sampled. To avoid edge effects, a cuboid steel sampler with an internal side length of 19, 16, 13, 10, and 7 cm at the bottom was positioned in the center of the plot at the sowing density of 36, 49, 64, 121, and 225 ind. m^{-2}, respectively. The target individual plant within the sampler was cut at the soil surface and then excavated to a depth of 30 cm below the ground, and the roots were washed free of soil. The amount of fibrous roots collected in the soil within each sampler was considered as individual root mass, as it was not possible to differentiate roots between neighboring plants, especially at high densities. Each plant was separated into leaves, stems, roots, and bulbs. Dry mass was determined after all samples had been oven dried to a constant mass at 80 °C.

Data analysis

Although a range of mathematical models have been proposed to describe the density effect (Bleasdale and Nelder 1960; Watkinson 1980; Vandermeer 1984), the reciprocal equation of yield–density effect developed by Shinozaki and Kira (1956) is widely used to describe asymptotic yield–density relationship in non-self-thinning monocultures:

$$Y = \frac{N}{a + bN}, \tag{1}$$

where Y is yield per ground area, N is density, and a and b are coefficients specific to growth stages. This reciprocal equation is based on the logistic theory of plant growth and explains the density effect fairly well in non-self-thinning populations over a wide range of densities. Since the reciprocal equation failed to describe unimodal yield–density relationship, Watkinson (1980) reparameterized the models of Bleasdale and Nelder (1960), which can describe both asymptotic and unimodal responses of stand yield to plant density at one point in time:

$$Y = \frac{w_m N}{(1 + aN)^b}, \tag{2}$$

where w_m, a, and b are fitted parameters. As above, w_m is the mass of an isolated plant in the absence of competition. Parameter a is defined as the ecological neighborhood of the species (in units of area), which is essentially the area an individual requires to achieve w_m (Watkinson 1980; Weiner and Freckleton 2010), and b is a dimensionless scaling parameter that determines the shape of the yield–density curve (Li et al. 1996); when $b = 1$, Eq. 2 is synonymous with the reciprocal equation of Eq. 1. The criteria for distinguishing the form of the yield–density curve are as follows: (1) when the lower 95 % confidence limit (LCL) of the estimated parameter b in Eq. 2 was <1 and the upper 95 % confidence limit (UCL) > 1, the curve is considered asymptotic; (2) when UCL < 1, the curve is increasing; and (3) when LCL > 1, the curve is unimodal (Li et al. 1996).

Non-linear regression based on the Levenberg–Marquardt method (Kelley 1999) was used to fit Eq. 2 as the base-line yield–density model, to the data on dry mass of aboveground parts, belowground parts, leaf, stem, root, and bulb over the four harvests. The yields of above- and belowground part were calculated by multiplying average shoot dry mass (=stem + leaf mass) and belowground dry mass (=bulb + root mass) by sowing density. Yield of an organ (leaf, stem, root or bulb) per area is the product of mean organ mass and population density. All data were analyzed with IBM SPSS statistical software (version 19.0, SPSS, Inc., Chicago, IL).

Results

Equation 2 provided a good fit to the data in all cases (Tables 1, 2).

Effects of density on aboveground parts

The three parameters, w_m, a and b, increased with time (Table 1). The aboveground yield–density curve given by Eq. 2 moved upwards over time (Fig. 1a), and CFY was reached only at the final harvest. At the early growth stages (17–49 days after sowing), aboveground yield increased monotonically with the increasing planting density, whereas the relationships between aboveground yield and density were asymptotic at the final harvest (65 days after sowing; $R^2 = 0.936$; Fig. 1a; Table 1). While the aboveground yield of high and very high density (H and HH) populations differed initially by days 17, 33, and 49, it became less different with time and eventually became constant by day 65 (Fig. 1a).

Effects of density on belowground parts

Populations showed a unimodal relationship between belowground yield and sowing density at 49 and 65 days ($R^2 = 0.812$ and 0.811, respectively; Fig. 1b; Table 1). However, from 17 to 33 days after sowing, the belowground yield increased monotonically with the sowing density (Fig. 1b; Table 1). As plants grew, the belowground yield–density curve moved upwards and shifted from the monotonically increasing to unimodal, indicating that an optimum density exists at the two later growth stages (49 and 65 days after sowing; Fig. 1b).

Effects of density on plant organs

Estimated parameters w_m, a and b of above- and belowground organs all increased over time (Table 2). The relationship between leaf yield and sowing density appeared to be asymptotic at 49 and 65 days ($R^2 = 0.846$ and 0.985, respectively), whereas the relationship is monotonically increasing at 17 and 33 days (Fig. 2a; Table 2). The time trend of leaf

Table 1 Results of parameter estimates for the model $Y = \frac{w_m N}{(1+aN)^b}$ for the four harvests (17, 33, 49, and 64 days after sowing), where w_m, a, and b are the estimated parameters (±SE), with respect to above- and belowground parts

Time (days)	Biomass component	Estimated parameters			R^2	Form of Y–N curve
		w_m	a	b		
17	Aboveground	2.14 ± 0.32	0.0025 ± 0.00082	0.50 ± 0.070	0.993	Increasing
33		2.70 ± 0.46	0.0064 ± 0.0012	0.90 ± 0.030	0.995	Increasing
49		3.93 ± 0.56	0.0090 ± 0.0023	0.82 ± 0.040	0.990	Increasing
65		5.95 ± 0.99	0.017 ± 0.010	1.07 ± 0.11	0.936	Asymptotic
17	Belowground	1.01 ± 0.12	0.0025 ± 0.00062	0.56 ± 0.010	0.997	Increasing
33		2.24 ± 0.30	0.0083 ± 0.0016	0.68 ± 0.010	0.989	Increasing
49		30.73 ± 2.39	0.20 ± 0.030	1.29 ± 0.19	0.812	Unimodal
65		63.04 ± 6.06	0.25 ± 0.050	1.36 ± 0.25	0.811	Unimodal

Table 2 Results of parameter estimates for the model $Y = \frac{w_m N}{(1+aN)^b}$ for the four harvests (17, 33, 49, and 64 days after sowing), where w_m, a, and b are the estimated parameters (±SE), with respect to organs (leaf, stem, root, and bulb)

Time (days)	Yield component	Estimated parameters			R^2	Form of Y–N curve
		w_m	a	b		
17	Leaf	0.65 ± 0.060	–0.00037 ± 0.00049	0.83 ± 0.040	0.994	Increasing
33		2.26 ± 0.25	0.0065 ± 0.00084	0.89 ± 0.070	0.996	Increasing
49		2.83 ± 0.45	0.010 ± 0.0019	0.95 ± 0.070	0.846	Asymptotic
65		4.68 ± 0.78	0.020 ± 0.013	0.99 ± 0.26	0.985	Asymptotic
17	Stem	0.32 ± 0.024	0.0018 ± 0.00087	0.54 ± 0.010	0.991	Increasing
33		0.58 ± 0.068	0.0056 ± 0.0025	0.67 ± 0.010	0.954	Increasing
49		0.68 ± 0.056	0.0061 ± 0.00063	0.86 ± 0.040	0.998	Increasing
65		0.99 ± 0.14	0.0076 ± 0.0019	0.90 ± 0.030	0.900	Increasing
17	Root	0.40 ± 0.073	0.0064 ± 0.0017	0.67 ± 0.020	0.986	Increasing
33		0.69 ± 0.069	0.014 ± 0.0051	0.70 ± 0.010	0.955	Increasing
49		0.71 ± 0.10	0.015 ± 0.0078	0.87 ± 0.050	0.945	Increasing
65		0.84 ± 0.18	0.016 ± 0.026	0.83 ± 0.020	0.805	Increasing
17	Bulb	0.52 ± 0.053	0.0016 ± 0.0014	0.73 ± 0.07	0.991	Increasing
33		1.35 ± 0.16	0.0066 ± 0.021	0.81 ± 0.050	0.992	Increasing
49		51.34 ± 11.27	0.46 ± 0.22	1.411 ± 0.13	0.817	Unimodal
65		60.50 ± 7.15	0.31 ± 0.14	1.54 ± 0.17	0.826	Unimodal

yield–density relationship was almost identical to that of the aboveground yield–density relationship, except that the leaf yield tended to reach constant values more rapidly than the yield of aboveground parts at an earlier stage in *A. cepa* var. *aggregatum* populations (Fig. 1a, 2a).

The stem yield increased monotonically with the increasing density at all growth stages (Fig. 2b; Table 2). The root yield–density curve also moved upwards over time, and the root yield increased monotonically with sowing density throughout the growing season (Fig. 2c; Table 2).

The trend over time for the relationship between bulb yield and sowing density was similar to that of the belowground yield–density relationship at each harvest (Fig. 1b,2d), since the bulb mass contributed to

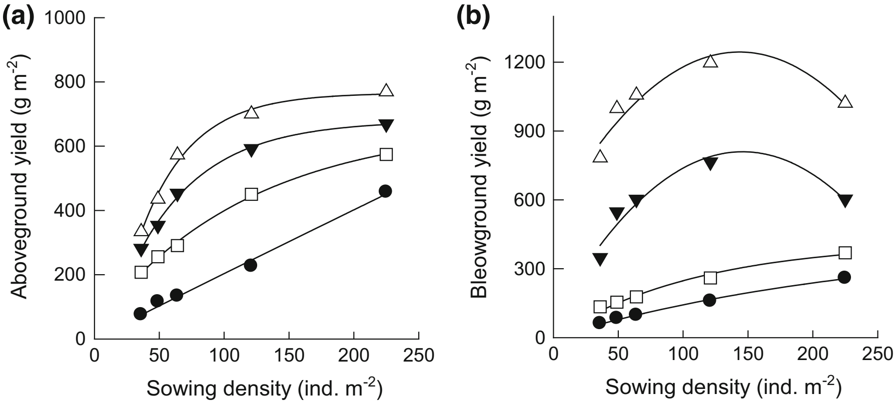

Fig. 1 Yield–density effect between **a** aboveground yield and density, and between **b** belowground yield and density. *Closed circles* 17-day-old, *open squares* 33-day-old, *closed inverted triangles* 49-day-old, *open triangles* 65-day-old. *Lines* are non-linear regression fits of the hyperbolic density–dependence model

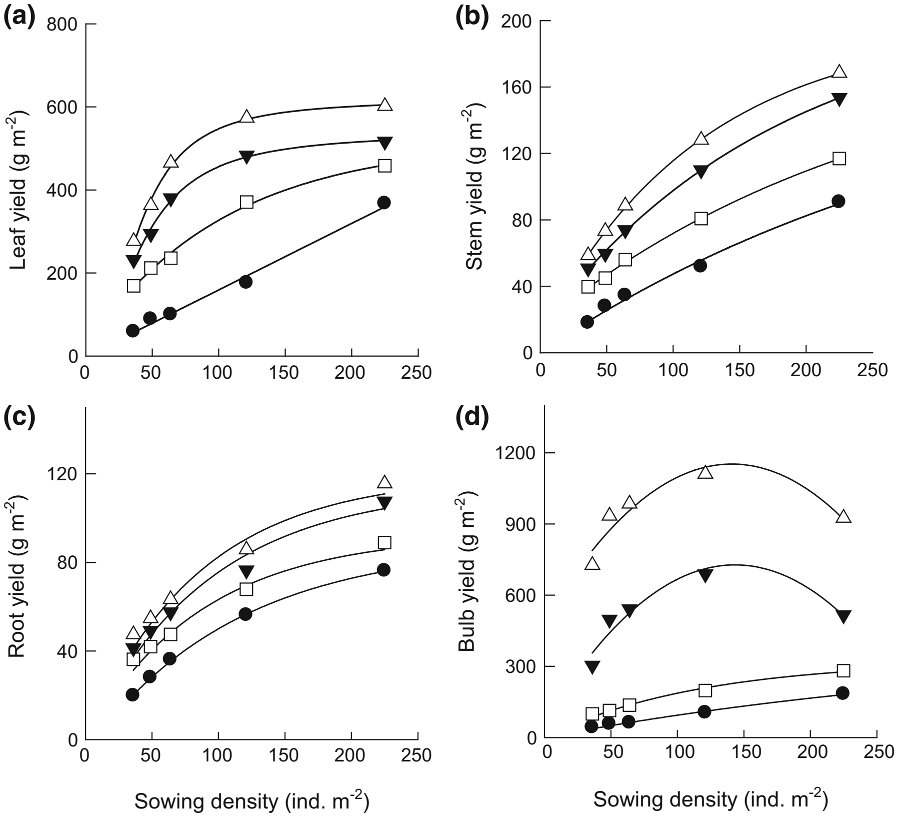

Fig. 2 Yield–density effect between organ yield and density: **a** leaf, **b** stem, **c** root, and **d** bulb. *Closed circles* 17-day-old, *open squares* 33-day-old, *closed inverted triangles* 49-day-old, *open triangles* 65-day-old. *Lines* are non-linear regression fits of the hyperbolic density–dependence model

most of the belowground mass (89–94 %) (Fig. S2 in Online Resource). A unimodal relationship between bulb yield and density is also seen at 49 and 65 days ($R^2 = 0.817$ and 0.826, respectively), whereas bulb yield increased monotonically with increasing density at 17 and 33 days (Fig. 2d; Table 2). The unimodal bulb yield–density curves indicated that there is an optimum density at late growth stages.

Discussion

Density effect in crowded, non-self-thinning populations

When parameter *b* in Eq. 2 is equal to 1.0, it results in CFY (Watkinson 1980). Our results present clear evidence for a constant amount of aboveground biomass per ground area, i.e., asymptotic total stand yield at high densities, in crowded but non-self-thinning populations of *A. cepa* var. *aggregatum*. Similar results have been obtained for some agricultural crops experiencing little mortality, e.g., *Solanum tuberosum* (potato; Holliday 1960), *Daucus carota* (Li et al. 1996), *Phaseolus vulgaris* (snap bean; Shirtliffe and Johnston 2002), and three out of four genotypes of *Cajanus cajan* (pigeonpea) grown in contrasting environments (Mligo and Craufurd 2007). This pattern has also been observed in the self-thinning stands of clonal grasses or woody plants, e.g., *Vulpia fasciculata* (Watkinson 1984), *Stipa tenacissima* (Ramírez and Bellot 2009), and *Pinus densiflora* (Xue and Hagihara 2008). From an evolutionary perspective, CFY occurs because competition for resources is an important determinant of plant fitness. If there are unused resources, and these resources are limiting the performance of individuals, those individuals that are better at capturing and utilizing these resources will have a selective advantage over those that are not as good at doing so (Weiner and Freckleton 2010).

While most studies on the sowing density effect are usually consistent with CFY, some studies on cultivated or wild species show decreases in total population biomass at high densities (Pretzsch 2003; Bagchi et al. 2010; Rahman et al. 2011). Documented exceptions to CFY occur when plant–plant interactions other than resource competition, such as allelopathy or facilitation among plants, predominate (Rice 1984; Chu et al. 2008).

Differences between above- and belowground yield–density relationships

The values of parameter *b* greater than 1.0 reflect the fact that increasing density leads to a less efficient use of the resources within a given area in terms of total dry matter production (Watkinson 1980). In our study, the estimated parameter *b* had statistically different values for above- and belowground yield by day 49 and 65, with the former approximates to 1.0 and the latter significantly greater than 1.0, indicating that distinct density responses of yield occur above- and belowground. The belowground yield was maximized at a certain density at the later growth stages (from 49 to 65 days)—a different trend from the case of aboveground yield. Li et al. (1996) also found decreases in belowground and total biomass of *Daucus carota* at high densities, and yet this was accompanied by a constant amount of shoot biomass. These findings were in line with fundamental differences between above- and belowground competition processes (Cahill 1999). Although root and shoot are functionally integrated, the spatial separation and obvious environmental differences created by the soil–air interface between them could lead to mechanistic difference between above- and belowground competition (McPhee and Aarssen 2001). More importantly, evidence is accumulating that, in contrast to competition for light above ground, competition for mineral nutrients and water below ground is generally size symmetric (Weiner et al. 1997). The mode of competition has been demonstrated to alter biomass–density relationships (Stoll et al. 2002). Under size-symmetric competition, less size variation develops and stand growth, including the growth of the larger individuals with large root systems, slows down. As a result, populations at higher density that are composed by many small individuals may produce less biomass belowground than somewhat lower densities, in which there are fewer larger individuals filling the same area. It is therefore likely that the processes and consequences of density effects for above- and belowground parts are different, resulting in different yield–density relationships.

Density effects on above- and belowground organs

Most early research was based on plant parts of economic value in agricultural settings, i.e., seed production and the yield of vegetative propagules. For example, unimodal density–productivity relationship has been documented for fruit or seed production (Willey and Heath 1969). Either asymptotic or unimodal response has been documented in vegetative yield to density, e.g., yields of tubers or bulbs (Holliday 1960; Willey and Heath 1969). Previous research is not one “body” of work but is spread around in several different research areas and contexts, e.g., plant population biology, agriculture, and horticulture. Very few of the studies have either investigated different yield responses to density for different functional organs as a whole, or rigorously tested whether there is a general yield–density pattern for above- and belowground organs.

The evidence for constant final leaf biomass in herbs is rare, although constant leaf biomass in fully closed forest stands has been reported (Ogawa 2008). Our results show asymptotic leaf yield–density relationship in *A. cepa* var. *aggregatum*, which is consistent with the constant leaf biomass per ground area as observed in *Brassica oleracea* var. *acephala* (kale) and *Camellia sinensis* (tea; Holliday 1960). Similarly, the maximum leaf biomass per unit area was independent of shoot density among 29 populations of temperate seagrass *Zostera marina* originating from 30°N to 56°N in Europe (Olesen and Sand-Jensen 1994). Constant final leaf biomass was also observed in overcrowded *Pinus densiflora* and mangrove (*Bruguiera gymnorrhiza*) stands (Xue and Hagihara 2008; Deshar et al. 2012). The leaf area index stayed constant in pure stands of *Trifolium pratense* and *Mercurialis perennis* as thinning proceeded, which may assure the maximum rate of photosynthesis in the canopy over time (Hutchings and Budd 1981). Thus, there is considerable evidence for the existence of a constant leaf biomass value for stands of a given species or mixed stands of a group of ecologically similar species after canopy closure. This may be because ever-increasing leaf area with the increasing density would mean that light levels reaching lower leaves in the canopy would be far below the compensation point. Therefore, many plants invest more in stems at high population density, so their leaves will be higher in the canopy, rather than increasing leaf biomass and therefore area. Because of their growth form, onions have a limited ability to increase leaf height with the increasing density, but they do so to the degree possible at the expense of leaf number (Fig. S1 in Online Resource), and this is still a better way of dealing with very high density than the increasing leaf biomass.

At different densities, stem mass contributed on average only 16–22 % to aboveground mass and the remainder was leaves (Fig. S2 in Online Resource). Therefore, the contribution of support structures (stems) to the yield–density relationship pattern for aboveground is probably much smaller than the contributions of photosynthetic organs (leaves). Maliakal et al. (1999) suggested that competition for light induces an increase in biomass allocation to stem, probably via phytochrome-mediated stem elongation. With the increasing height, plants have to prioritize investment in support tissue to maintain mechanical stability (McMahon 1973). Increased stem elongation in response to the presence of neighbors acts as a strong sink. As a result, stem yield is likely to increase monotonically with increasing population density.

Studies of relationship between vegetative components of yield and population density of different plant species have produced conflicting results. Some experiments showed that those forms of yield which constitute a vegetative reproductive part of the crop conformed to an asymptotic relationship, e.g., tuber yield of *Solanum tuberosum* (Holliday 1960), root tuber yield of *Beta vulgaris* (long beet; Warne 1951) and *Pastinaca sativa* (parsnip; Bleasdale and Thompson 1966), and bulb yield of *Tulipa gesneriana* (tulip; Rees and Turquand 1969). However, yield of vegetative propagules in some species may also show a unimodal relationship with density, e.g., root tuber production of *Beta vulgaris* (globe red beet; Willey and Heath 1969) and *Daucus carota* (Li et al. 1996). In the present study, the bulb yield was maximized at an intermediate density at the later growth stages (49–65 days after sowing). Similarly, bulb yield of *Allium cepa* L. increased with the increasing density until an optimum was reached and thereafter the yield declined (Bleasdale 1966; Rumpel and Felczynski 2000). At high densities, plants compete for resources and bulbs mature at a smaller size. Bulb yield declines because mature bulb size per individual decreases faster than the number of individuals per area increases. An alternative hypothesis is that plants preferentially allocate resources to the organs responsible for acquiring the most limited resource (Shipley and Meziane 2002). Plants grown at higher densities are "thinner" at a given height than they would be at lower density, and they allocate proportionately more biomass to shoot as to maximize the interception of light (Maliakal et al. 1999). Therefore, an optimum density for the bulb yield may exist, and the bulb yield–density pattern had a strong effect on that for belowground yield–density because of the large amount of bulb mass compared with the root mass (Fig. S2 in Online Resource). However, the optimum density for bulb biomass production is not optimum for the farmer because of the higher value of larger bulbs, since the farmer's objective is to obtain high proportion of large bulbs, not maximum total biomass (Bleasdale 1966; Rees and Turquand 1969; Rumpel and Felczynski 2000).

There is no optimum density maximizing root yield—root yield increased monotonically with increasing population density. The main function of plant roots is the acquisition of mineral nutrients and water from the soil. This pattern probably arises because roots actively forage for nutrients (Hodge 2004) and avoid patches where root densities of competing neighbors are high (Gersani et al. 1998). Individuals in crowded populations allocate relatively more aboveground biomass to stems and petioles, but an increase in stem biomass will be at the expense of leaves and not roots (i.e., density did not affect root:shoot ratio but can alter relative allocation between stems and leaves; Casper et al. 1998). Consequently, root yield increased monotonically with the increasing population density.

In conclusion, classical constant final yield does not apply to the yield–density relationships of all plant parts, and the aboveground structures were more likely than those belowground to show constant final yield, perhaps due to the different mechanisms of competition above- versus below ground. Since below- and aboveground parts are integrated, we should pay attention to the dynamics of both. There are many more factors to consider in natural than in agricultural populations, since the former exist in multispecies communities consisting of species with different strategies, in which spatial heterogeneity is much greater and there is less synchrony in germination and growth. Despite these differences, single-species populations are the starting point for the study of density dependence in nature as well as in agriculture.

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