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Effects of breeding on the performance of oat (*Avena* spp.) on experimental resource gradients

MSc thesis

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Tartu 2005

Contents

1. Introduction

Despite the strong selection for high yield in monocultures, some modern crops seem to retain the agronomically undesirable patterns of response to stress that characterized their uncultivated ancestors. The petiole and stem elongation response to crowding might reduce assimilate availability for agriculturally more productive activities, such as root, grain, or fruit growth, and might increase crop susceptibility to lodging. If this is correct, rendering a plant insensitive to neighbour presence should pay off in terms of reduced wasteful allocation (Smith, 1992; Robson et al., 1996; Ballaré and Casal, 2000). However, plastic responses to light availability also have a number of desirable effects on whole-canopy growth and crop yield. These effects involve delay in the development of size inequalities in plant populations, a more efficient arrangement of canopy leaf area with respect to the distribution of light gaps and, consequently, the better ability of plants to "forage" for light, reduce in unproductive tillering at high densities, and physiological acclimation to the canopy environment, such as leaf senescence and the concomitant redistribution of leaf nitrogen and photosynthetic capacity (Ballaré et al., 1994; Ballaré and Scopel, 1997; Rousseaux et al., 1997). Additionally, at the individual level, plasticity in various physiological and morphological traits is known to optimise the capture of different resources in a manner that maximizes plant growth (optimal partitioning models; see e.g., Johnson and Thornley, 1987). Due to these considerations, the cost of losing plasticity may greatly outweigh the potential allocation benefits of a suppressed shade-avoidance response.

With current pressure to reduce the economic and environmental costs of weed management and the spread of herbicide-resistant weeds, the innate ability of cereal crops to suppress weed growth has become increasingly important (Christensen, 1994; Seavers and Wright, 1999; Jannink et al., 2000; Baumann et al., 2001; Didon, 2002; Vandeleur and Gill, 2004). It has also been recognised that modern crop plants tend to be selected on the basis of high yields and resistance to pests and diseases, whereas their competitive abilities are ignored (Lemerle et al., 1996; Olofsdotter et al., 2002). Comparisons between various cultivars showed that there are significant differences

in weed-suppression ability between varieties and no clear correlation between yield and competitiveness, suggesting that both characters could be improved by breeding (Christensen, 1994; Lemerle et al., 1996; Seavers and Wright, 1999; Weiner et al., 2001).

The specific pattern of interactions between a given genotype and environmental conditions (norm of reaction) has evolved in response to numerous selection pressures and constraints. Little is known about how the alterations of the mechanisms controlling plasticity of an individual plant to a given environmental signal influence the functioning and productivity of the plant community as a whole (Schmitt et al., 1986; Schmitt et al., 1995; Ballaré and Scopel, 1997; Ballaré et al., 1997; Ballaré and Casal, 2000; Callaway et al., 2003). Probably, natural selection will operate to advance plastic genotypes if plasticity confers individual competitiveness. However, natural selection has few, if any, direct mechanisms to optimize the community performance (e. g., high grain yield per unit land area) when collective performance conflicts with individual fitness (Harper, 1977; Schieving and Poorter, 1999; Zhang et al., 1999; Gersani et al., 2001; Denison, 2003; Falster and Westoby, 2003; Weiner, 2003). On the contrary, the main objective of plant breeding by humans is overall community production, not individual performance. Therefore, we can assume that unintentional changes in plants plasticity during long-term breeding could occur as a consequence of selecting for high yields in agricultural systems.

Available data suggests that the huge increases in yields due to the development of new cultivars during the 21st century can be mostly attributed to changes in biomass allocation. Plant breeding has not resulted in increased primary production in the field, but the success was mainly achieved through selecting for high Harvest Index, i.e. high allocation to reproductive structures at the expense of leaves and stems, which has often resulted in a decrease in the competitive ability of modern crops (Evans and Fischer, 1999; Peng et al., 2000; Denison et al., 2003; Weiner, 2003; Vendeleur and Gill, 2004). However, the effects of long-term agricultural breeding on plant plasticity have not been investigated extensively. Similarly, it would be valuable to know the overall effect of unidirectional breeding on plant ontogeny, and an understanding of the mechanisms behind the high yield potentials of modern crops could have important implications for further plant breeding.

The breeding process can be treated as a long-term selection experiment, where high mean yield is the main target of selection. Any genetic correlations of the target

trait with other traits are likely to show up as correlated responses to the selection (Scheiner, 2002; Brakefield, 2003). Our main objective in the present study was to investigate the effects that long-term breeding (intense selection for high yield) could have on the ability of plants to respond to different levels of light and nutrient availability. Our special interest was to examine to what degree has phenotypic plasticity been subject to indirect unidirectional selection, and to what degree have genetic constraints limited the evolution of the plasticity of ecologically important traits in breeding.

Plant responses to environmental variation frequently include both reduced growth rate under resource limitation, as well as active changes in whole developmental program that are assumed to enhance performance and resource acquisition in various conditions (Sultan and Bazzaz, 1993; Coleman et al., 1994; Sultan, 1995; McConnaughay and Coleman, 1999; Dorn et al. 2000; Wright and McConnaughay, 2002). Therefore, it was important in our experiment to distinguish between passive plasticity (phenotypic change in a predictable way as a function of plant growth or development), and ontogenetic/developmental plasticity (variation in the ontogenetic trajectory of a trait induced by environmental change; Wright and McConnaughay, 2002). We investigated four oat (*Avena sativa* L.) varieties of different age (originating from 1930, 1952, 1980 and 1999) to look at the effects of breeding. Phenotypic plasticity of common wild oat (*A. fatua* L.) and its interactions with the oldest (originating from 1930) and the youngest oat varieties (originating from 1999) were also examined to compare cultivated oats with their wild ancestor. The potential effects of breeding on the competitive abilities of the varieties were investigated in field trials.

2. Materials and methods

2.1.Study species

Four varieties of *Avena sativa,* originating from different years, were selected for examination - Kehra varajane, Hämarik, Viker and Villu, introduced in the years 1930, 1952, 1980 and 1999, respectively. In the following text the varieties will be referred to as V-1930, V-1952, V-1980 and V-1999. All the varieties have been bred in Estonia. German, Belgian and Swedish cultivars were used in the breeding process. The three earliest varieties are closely related to one another, while V-1999 is not. The main breeding aims were high yield capacity, high 1000 kernel weight, low husk content, high volume weight and grading, good lodging and disease resistance (Pill, 1930; Laurson, 1980; Tamm, 1998, 1999).

In order to compare the growth of studied oat varieties with their wild ancestor, *Avena fatua* L. was included in experiments in 2004 (Eichwald et al., 1978).

2.2. Garden experiments

Seeds of the four oat varieties were obtained from the Jõgeva Plant Breeding Institute, Estonia. The seeds were sown on perlite in a greenhouse on June 14, 2003. After a week, 40 seedlings of each variety were planted into 1.2-litre plastic pots (diameter 7 cm, height 31 cm) filled with fine sand. The planted seedlings were randomly distributed among four shading treatments (100, 50, 25 and 10 % of full daylight) and two nutrient treatments (0.78 mg N, 0.23 mg P, 0.97 mg K and microelements per plant twice a week in the low nutrient treatment and four times as much in the high nutrient treatment). There were thus 5 replicate plants per each treatment variant. Shade was provided using tents made of aluminium-coated shade cloths (spectrum neutral; Ludvig Svensson, Kinna, Sweden). Water stress was avoided by combining constant bottom watering (height of water table 15 cm) and daily automatic top

watering. The plants were harvested at the beginning of August, 2003. It was not possible to delay harvesting since plants of the darkest treatment were severely stressed and would have withered by autumn. Out of the total of 160 cultivated plants six died before harvesting. Since all individuals were harvested at maturity, the observed patterns of trait covariation show relationships among different individuals at one point in time (static inter-individual allometry) and may be different from those of a single individual over the course of growth (Weiner and Thomas, 1992; Coleman et al., 1994).

In summer 2004, an additional experiment was undertaken with plants of *A. fatua* to assess its plasticity to light availability. Seeds were obtained from a commercial source. The same light treatments were used in the experiment (100, 50, 25 and 10% of full daylight). All plants were fertilized twice a week as plants from high nutrient treatment in the former experiment. There were 15 replicates per each light treatment. Five randomly chosen plants were harvested at three successive dates (July 19, August 9, and August 30) to describe plants' ontogenesis.

2.3. Field experiment

Two oat (*Avena sativa* L.) varieties (V-1930 and V-1999 introduced in the years 1930 and 1999, respectively) and common wild oat (*A. fatua* L.) were grown in the field either in monocultures of three sowing densities (300, 500, and 700 seeds m^{-2}) or in mixtures (V-1999/V-1930, Fatua/V-1999, and Fatua/V-1930). Germination probability of 90% (reported by seed suppliers) was taken into account in determining seed number sowed per m^2. In addition, a number of single plants were grown at the edge of the field to describe the growth of plants in full daylight without competition. The experiment was run from June to August 2004, in Tartu, Estonia. The field was treated with herbicide mixture, and was fertilized with N70 P16 K29 (kg ha^{-1}) before sowing. Plants were grown in stands of 2.25 m^2, and there were two replicates per each treatment. Seeds were sown in a regular pattern, distance between seeds in a row and between rows being equal. Treatments were randomly distributed within the field.

Four plants from each replicate of monocultures and three plants per variety from each replicate of mixed stands were harvested at three subsequent dates (July 19, August 9, and August 30) for morphometrical analysis. At the end of the experiment,

above-ground biomass from 0.25 m^2 area in the centre of each replicate was harvested to assess final plant densities and biomass production per unit land area.

Interception of PAR (photosynthetically active radiation) by plant canopies was measured using linear light meter (Licor LI-250) at every harvest. Since lodging in the end of experiment could bias estimates of light interception by plant canopies, light measurements at the last harvest were not included in the analysis.

2.4. Plant measurements

For each plant, the number of leaves was recorded. Stem length, leaf length and maximum leaf width were measured to the nearest half millimetre. Then plants were separated into panicles, leaves, stems and roots, dried at 75°C for 48 hours, and weighed to an accuracy of 10^{-6} kg.

Specific leaf mass *SLM* (leaf dry mass per unit leaf area, kg m^{-2}) was calculated using the measured characteristics. Given that preliminary analysis revealed a very strong correlation (R = 0.96) between leaf area estimates achieved by a) measurements using a scanner (CanonScan LIDE 30), Adobe Photoshop 7.0 and Pindala 1.0 software, and b) calculations using leaf length and leaf width data, the less laborious method – calculation – was used.

Number of plants and tillers were counted in samples of above-ground biomass from 0.25 m^2 land area at the end of the field experiment. Samples were separated into panicles, stems, and leaves, dried at 75°C for 48 hours, and weighed to an accuracy of 10^{-4} kg.

2.5. Data analysis

To improve normality and homogeneity of variances, all dependent variables were ln-transformed before analysis, except for panicle mass, which was square-root transformed to achieve linear relationship with biomass. As there is no need to differentiate between isometry and allometry in our study, we use the term "allometry" throughout, referring to both (Gould, 1966).

Second order polynomial regression analysis, applied on ln-transformed data, was used to test for deviations from linearity in the allometric relationships and in the

reaction norms examined. A significant second order polynomial term was considered as evidence of a curvilinear relationship. Since the quadratic term for biomass was significant only for stem length *vs.* total biomass relationship in oat varieties (*A. sativa*), the quadratic term was not included in the analysis of the remaining traits.

General linear models were adopted to assess plants' plasticity and allocational patterns in different oat varieties and wild oat. Leaf length, leaf width, mean leaf area, total leaf area, mean leaf mass, total leaf mass, *SLM*, stem length (in wild oats only), stem mass, root mass, panicle mass, and number of leaves were examined as dependent variables. Variety (*V*), fertilization (*N*), and light availability (*L*) were used as independent predictors if oat varieties were studied; only light availability could be included if wild oat was examined. Biomass (*B*) was included in models as a covariate. Two-way interactions between all predictor variables (independent variables and covariate) were studied.

Whenever trait values vary as a function of plant size (total biomass), and plant final size is dependent on light and nutrient availability, the trait will exhibit passive plasticity in response to changes in the levels of these resources (Wright and McConnaughay, 2002). Thus, a significant biomass (*B*) term in the linear model should indicate the presence of passive plasticity in a given trait. It is important to note here that if we studied allometric relationships between different biomass components (e.g. leaves *vs* stems or shoots *vs* roots), only an allometric slope $\neq 1$ in log-log scale would indicate passive plasticity (McConnaughay and Coleman, 1999; Müller et al., 2000). In our case (biomass component *vs* total biomass is studied), total biomass is to a certain extent equivalent with the ontogenetic phase and any difference in absolute value of a trait due to biomass effect can and should be treated as a passive plastic response.

Ontogenetic plasticity, as defined by changes in the intercept and/or slope of the relationship between a trait and total biomass in response to variation in light or nutrient supply, is indicated by the significance of *L, N, L*B* or *N*B* terms in the linear model. Significant *V, V*N,* and *V*L* terms denote differences in trait means between varieties. Substantial variation in allometric slopes between varieties is identified by a significant *V*B* term.

Differences between trait means were assessed using Tukey's HSD test or Fisher's LSD test (Sokal and Rohlf, 1995). We used a sequential Bonferroni criterion to correct for multiple tests (Sokal and Rohlf, 1995).

3. Results

3.1. Garden experiments
3.1.1. Oat (A. sativa L.) varieties
3.1.1.1. Plant biomass and stem elongation

The dependence of stem length on light availability was non-linear in all varieties (quadratic term for light, significant at $P < 0.0012$; linear term for light, also significant; Fig. 1B in I) but there was no evident effect of fertilization (neither main effect nor interaction with light). It is clearly seen from the figure that the two earlier varieties (V-1930 and V-1952) produced significantly shorter stems in full daylight than in 50% shade while the two modern ones did not. In the darkest treatment there were no differences in biomass among varieties (Fig. 1A in I). At the same time there was difference between stem lengths of V-1980 and V-1999 at 10% light – the latter were significantly shorter (Fig. 1B in I).

The relationship between total biomass and stem length was, in most varieties, non-linear (except in V-1952) with a significant linear component (Table 1 in I). However, the degree to which plant height was predictable through total biomass differed greatly among varieties. In V-1952, biomass described only 12.5% of variation in stem length, while, in V-1999, as much as 76.3% of variation in plant height was attributable to plant total biomass (Table 1 in I).

3.1.1.2. Phenotypic plasticity in response to light and nutrient supply

All varieties displayed significant ontogenetic plasticity in traits associated with light interception - leaf length, leaf width, mean leaf area, and total leaf area (L and/or $L*B$, significant, Table 2 in I). An example of a typical response pattern in these traits is presented in Fig. 2 in I – the intensity of allocation into leaf area decreases with better light availability and there is less leaf area per given plant biomass. There was no

indication of any ontogenetic plasticity of leaf mass to light availability in our data. Specific leaf mass (*SLM*) increased under high light as a function of both plant size (passive plasticity; significant *B* term in Table 2 in I) and light availability (ontogenetic plasticity; significant *L* term in Table 2 in I; Fig. 3 in I).

The analyses of allocation patterns revealed that, in response to nutrient availability, plants altered leaf mean mass *vs.* total biomass and leaf total mass *vs.* total biomass allometries (significant *N*B* interaction, Table 2 in I; Fig. 4 in I). Root mass *vs.* total biomass allometry was changed slightly by both environmental cues (Fig. 5 in I). In general, allocation to roots increased and leaf area decreased under high light. Nutrient stress resulted in decreased allocation to leaf mass with a concomitant increase in root production.

3.1.1.3. Allometry

Allometric analysis of biomass partitioning revealed that modern varieties allocated relatively more above-ground biomass to panicles – the slope of the panicle mass *vs.* total biomass relationship was the greatest in V-1999, contrasting with other above-ground biomass characteristics, for which allometric slopes decreased towards V-1999 (in all cases *V*B* interaction significant, Table 2 in I; Fig. 8 in I).

3.1.2. Common wild oat (A. fatua L.)

Similar to cultivated oats, wild oat was able to adjust its leaf area and root allocation in response to varying light conditions (significant *L* or *L*B* terms in Table 1). Also no ontogenetic plasticity in stem mass and panicle mass was observed (terms *L* and *L*B* not significant in Table 1). However, some differences in other plant measures were revealed.

Differently from cultivated oats, wild oat exhibited ontogenetic plasticity to light availability in allocation to leaves: leaf mass production was more intense under low light conditions as compared to full daylight (Table 1; Fig. 1). Also plants produced leaves with lower mass density in shade than in full daylight independent of plant biomass (significant *L* term and not significant *B* term in Table 1).

Wild oat showed pronounced ontogenetic plasticity in stem length in response to varying light conditions (significant *L* term in Table 1). Plants elongated their stems

most intensively in the shadiest treatment and gradually reduced stem elongation as light conditions became favourable (Fig. 2).

Allocation to panicles in wild oat was very variable, and was not dependent on plant size (term *B* in Table 1 not significant). This contrasts to highly biomass-dependent allocation to reproduction observed in cultivated oats (Table 2 in I).

Table 1. Results of the ananlysis of the effects of light availability (*L*) and total dry biomass (*B*) on 12 morphological traits of common wild oat *(Avena fatua* L.).

	L	*B*	*L * B*	R2 adj.
Leaf length	**<0.001**	**<0.001**	0.372	**0.832**
Leaf width	0.089	**<0.001**	**0.003**	**0.856**
Mean leaf area	**<0.001**	**<0.001**	**0.006**	**0.900**
Total leaf area	**<0.001**	**<0.001**	**0.004**	**0.977**
Mean leaf mass	0.863	**0.025**	**<0.001**	**0.867**
Total leaf mass	0.927	**0.003**	0.034	**0.921**
Specific leaf mass	**0.023**	0.088	0.068	**0.830**
Stem length	**<0.001**	**<0.001**	0.116	**0.721**
Stem mass	0.126	**<0.001**	0.240	**0.967**
Root mass	**<0.001**	**<0.001**	**0.010**	**0.985**
Panicle mass	0.472	0.341	0.058	**0.670**
Number of leaves	0.018	**<0.001**	0.354	**0.514**
Df.	3	1	3	

All trait values were ln-transformed, except for panicle mass, which was square-root transformed. *P*-values are shown. Boldface indicates significant (*P* < 0.05) effects under sequential Bonferroni criterion. *Df.*: degrees of freedom, $R^2adj.$: adjusted determination coefficient. *n* = 60.
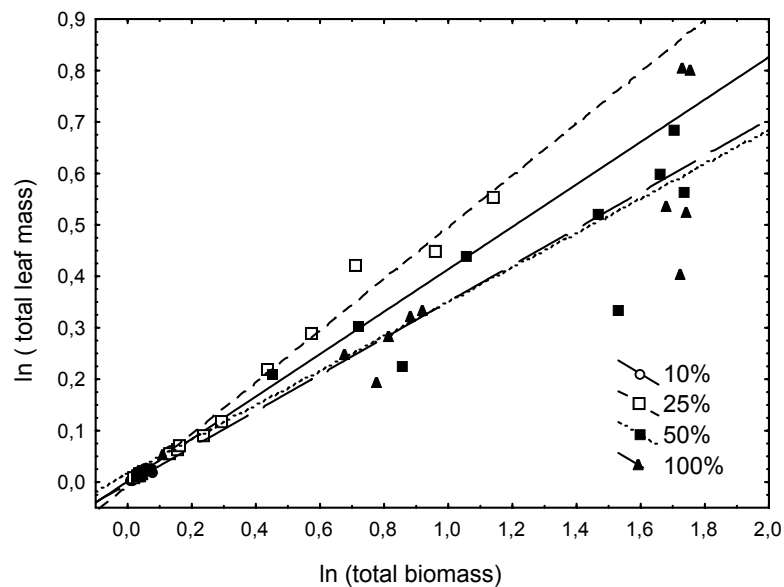
Fig. 1. Allometric relationships between leaf mass and total dry biomass for *A. fatua* in different light treatments (shown as percent of full daylight).
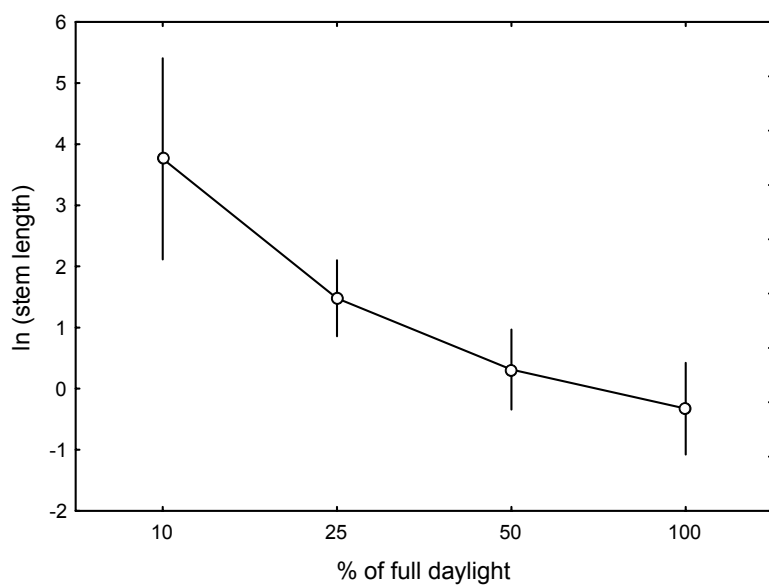
Fig. 2. Effects of light availability (shown as percent of full daylight) on stem lengths in common wild oat (*A. fatua*). Least-square means adjusted for mean plant biomass are shown. The error lines denote 95% confidence intervals for the mean.

3.2. Field experiment

3.2.1. Light interception and final plant densities

Germination of seeds of the two oat varieties was similar (73% and 70% for V-1930 and V-1999, respectively), but was considerably lower than expected 90% germination. Moreover, wild oat showed even poorer germination (50%). Due to different germination and growth patterns of oat varieties and wild oats, final plant densities and light interception by the canopies at the first measurement were different among varieties (Table 2, 3). Also, the seeds of the two oat varieties were significantly heavier than the seeds of wild oat (34.2 mg, 34.6 mg and 17mg for V-1930, V-1999 and wild oat, respectively; effect of plant identity significant at $P < 0.001$).

Although plants of *A. fatua* intercepted considerably less radiation at the first measurement than the two oat varieties, there was no effect of variety or sowing density on light interception by the time of the second sampling: canopies captured more than 95% of available light (Table 2). Despite low plant densities in stands of *A. fatua*, extensive tillering in monocultures of wild oat allowed it to produce as much tillers per square meter as in the dense stands of *A. sativa* (Table 3, Fig. 3).

Table 2. Light interception (% of PAR) in canopies of two oat (*Avena* sativa L.) varieties and common wild oat (*Avena fatua* L.) grown in monocultures at different densities and in mixtures.

variety	sowing density	time1		time2	
V-1930	300	91.6	de	97.7	de
V-1930	500	95.7	de	98.4	e
V-1930	700	95.7	de	98.4	e
V-1999	300	73.5	c	97.7	de
V-1999	500	89.6	d	98.5	e
V-1999	700	95.7	de	99.2	e
Fatua	300	28.6	a	95.8	de
Fatua	500	31.9	ab	96.4	de
Fatua	700	39.1	b	97.2	de
V-1930 + V-1999	700	94.6	de	98.6	e
Fatua + V-1930	700	92.5	de	98.5	e
Fatua + V-1999	700	92.4	de	97.9	e

time1: light interception at the first sampling; *time2*: light interception at the second sampling. Means within the same column followed by the same letter do no differ significantly at the $P < 0.05$.

Table 3. Plant densities and numbers of tillers per square meter in different experimental stands at the end of experiment. Total plant densities in the mixed stands are given in parentheses.

variety	sowing density	final plant density		final tiller density	
V-1930	300	278	**bcde**	388	**bcde**
V-1930	500	422	**efg**	544	**defg**
V-1930	700	578	**g**	725	**g**
V-1930	350*Fatua + 350*V-1930	316 (397)	**cde**	469	**cdef**
V-1930	350*V-1999 + 350*V-1930	278 (522)	**bcde**	325	**abcd**
V-1999	300	219	**abcd**	453	**cdef**
V-1999	500	356	**def**	588	**efg**
V-1999	700	509	**fg**	603	**efg**
V-1999	350*Fatua + 350*V-1999	313 (391)	**cde**	472	**cdef**
V-1999	350*V-1999 + 350*V-1930	244 (522)	**abcd**	288	**abc**
Fatua	300	75	**a**	613	**efg**
Fatua	500	131	**ab**	747	**g**
Fatua	700	163	**abc**	697	**fg**
Fatua	350*Fatua + 350*V-1930	81 (397)	**a**	109	**a**
Fatua	350*Fatua + 350*V-1999	78 (391)	**a**	141	**ab**

Means within the same column followed by the same letter do no differ at the P < 0.05.
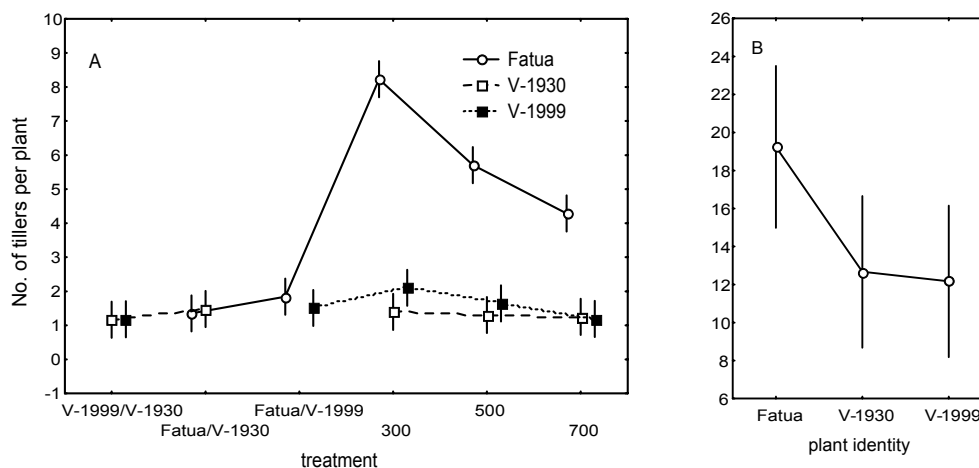
Fig. 3. Tillering of two oat varieties (*A. sativa*) and common wild oat (*A. fatua*) in A) monocultures of three sowing densities (300, 500, 700 seeds m^{-2}) and pairwise mixtures (350 seeds m^{-2} of each variety), and B) in single-grown plants. The error lines denote 95% confidence intervals for the mean.

3.2.2. Relative growth rates (RGR)

At the first sampling, plants of oat varieties had similar above-ground biomass independent of experimental treatment. Wild oat achieved substantially lower biomass by the first sampling as compared to cultivated oats (Table 4). Interestingly, wild oat performed best in the mixture with V-1999 where plant size of wild oat did not significantly differ from that of V-1999 (Table 4).

Between the first two samplings, oat (*A. sativa*) plants grown in dense stands exhibited significantly lower growth rates (*RGR*) as compared to single-grown plants (Table 4). Sowing density did not significantly influence the *RGR* of any of the oat varieties as well as wild oat grown in monocultures. Wild oat showed significantly higher growth rates in monocultures at all densities as compared to varieties of cultivated oat, and exhibited the same growth rates as cultivated oats in mixed stands.

All plants had the same growth rates between the next two samplings.

Table 4. Mean plant above-ground biomass at the first sampling (g) and relative growth rates (g g^{-1} per growth period) of two oat (*Avena sativa* L.) varieties (V-1930 and V-1999) and common wild oat (*A. fatua* L.) in different experimental stands.

variety	sowing density	B		RGRI		RGRII	
V-1930	single	0.910	e	17.03	cde	3.29	a
V-1930	300	0.695	de	4.48	ab	1.50	a
V-1930	500	0.459	de	4.94	abc	2.28	a
V-1930	700	0.440	cde	7.79	abcd	1.20	a
V-1930	350*(V-1999 + V-1930)	0.445	bcde	5.95	abc	1.83	a
V-1930	350*(Fatua + V-1930)	0.588	de	6.30	abcd	1.24	a
V-1999	single	0.615	de	17.66	de	2.81	a
V-1999	300	0.471	de	4.79	abc	1.74	a
V-1999	500	0.476	de	3.90	ab	1.74	a
V-1999	700	0.577	de	2.89	a	1.68	a
V-1999	350*(V-1999 + V-1930)	0.316	abcd	5.26	abc	1.37	a
V-1999	350*(Fatua + V-1999)	0.582	de	4.19	ab	2.09	a
Fatua	single	0.178	a	41.81	e	3.62	a
Fatua	300	0.175	ab	17.18	de	3.37	a
Fatua	500	0.191	a	15.76	cde	2.57	a
Fatua	700	0.223	abc	19.31	de	2.06	a
Fatua	350*(Fatua + V-1930)	0.199	abc	5.32	abc	1.33	a
Fatua	350*(Fatua + V-1999)	0.359	abcd	5.42	abcd	1.99	a

B: mean plant dry biomass at the first sampling; *RGRI*: relative growth rate between the first and second samplings; *RGRII*: relative growth rate between the second and third samplings. Means within the same column followed by the same letter do no differ significantly at the P < 0.05.

3.2.3. Vertical growth

Analysis of variance of plant shoot lengths revealed the highly significant three-way interaction between sampling time, treatment, and variety (P < 0.001). At the first sampling, *A. fatua* had significantly shorter shoots in all stands as compared to the two oat varieties, except the mixture of wild oats and V-1999 where wild oats were as tall as their competitors (Fig. 4A). By the end of the experiment, wild oats that grew in dense stands reached the same heights as plants of V-1930 and even slightly overtopped plants of V-1999 (Fig. 4C). At the first two samplings, single-grown plants of *A. sativa* were significantly shorter than plants grown in dense stands, but plants achieved equal heights by the end of the experiment (Fig. 4). There were no significant differences in vertical growth of *A. sativa* among the three sowing densities at any time. Initially not significant differences in shoot heights between V-1930 and V-1999 became more obvious by the end of the experiment. At the third sampling time, V-1999 had substantially shorter shoots in monocultures as well as in mixtures as compared to the other oat variety, the difference being particularly large in the mixture of V-1930 and V-1999 (Fig. 4C).

3.2.4. Total biomass, panicle mass and leaf area

In the mixed stand of V-1999 and V-1930, plants of V-1999 produced less panicle mass and less above-ground biomass per land area than V-1930 (Fig. 4). However, the two varieties performed equally well in monocultures of the three sowing densities used in the experiment. Wild oat achieved the same above-ground biomass as the two oat varieties in monocultures, but produced less biomass in mixed stands (apparently caused by poor germination). In all treatments, wild oat produced less panicle mass than V-1999 and V-1930. Wild oat performed better when grown mixed with V-1999 than when grown in the mixture with V-1930 (Fig. 4).

Although monocultures of *A. fatua* produced as much above-ground biomass per unit land area as cultivated oats did, panicle mass of wild oat per unit land area was less than in cultivated oats (Fig. 4). Instead of panicle production, wild oat produced more leaf area per given above-ground biomass as compared to cultivated

oats (variety*biomass interaction significant at $P < 0.001$ for both leaf area and panicle mass; Fig. 5). As has already been shown in the pot experiments, wild oat showed more variation in allocation to panicles (Fig 5B).
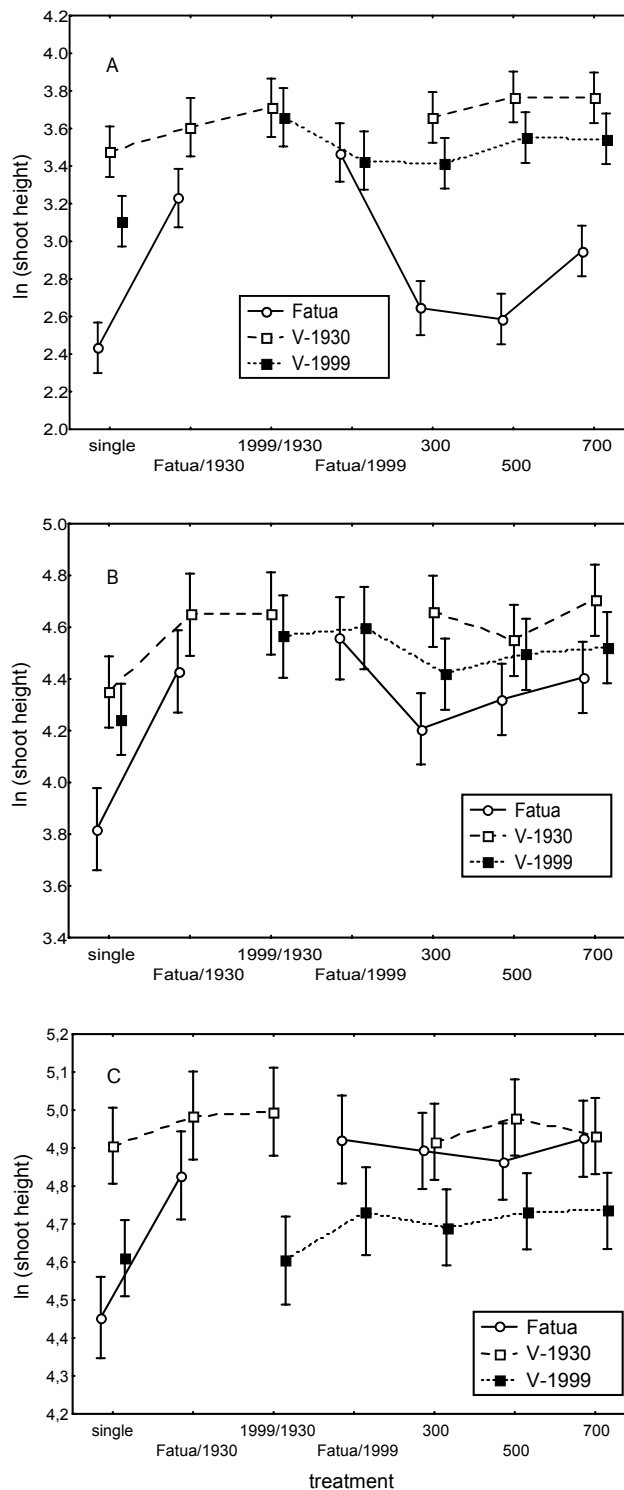
Fig. 4. Mean shoot height ($x10^{-2}$ m) at three sampling times (A - July 19, B – August 9, C – August 30) for two oat (*A. sativa*) varieties and common wild oat (*A. fatua*) grown at different densities (single, 300, 500, 700 seeds m^{-2}) in monocultures and mixed stands (700 seeds m^{-2}). Vertical bars denote 95% confidence intervals.
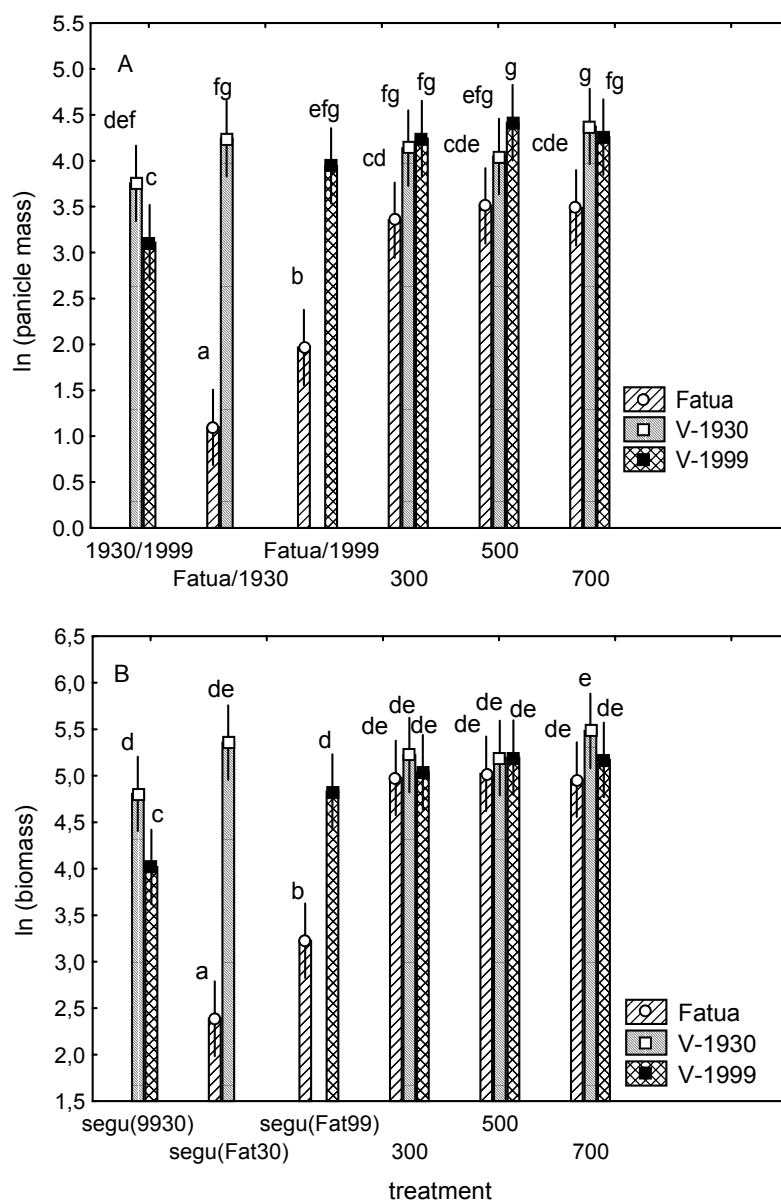
Fig. 5. Mean panicle dry mass per 0.25 m^2 (A) and above-ground dry biomass per 0.25 m^2 (B) for two oat (*A. sativa*) varieties and common wild oat (*A. fatua*) grown in monocultures of three different sowing densities (300, 500, 700 seeds m^{-2}) and in mixed stands (350 + 350 seeds m^{-2}). Lines denote 95% confidence intervals for the mean. Different letters indicate significant differences at the P < 0.05.
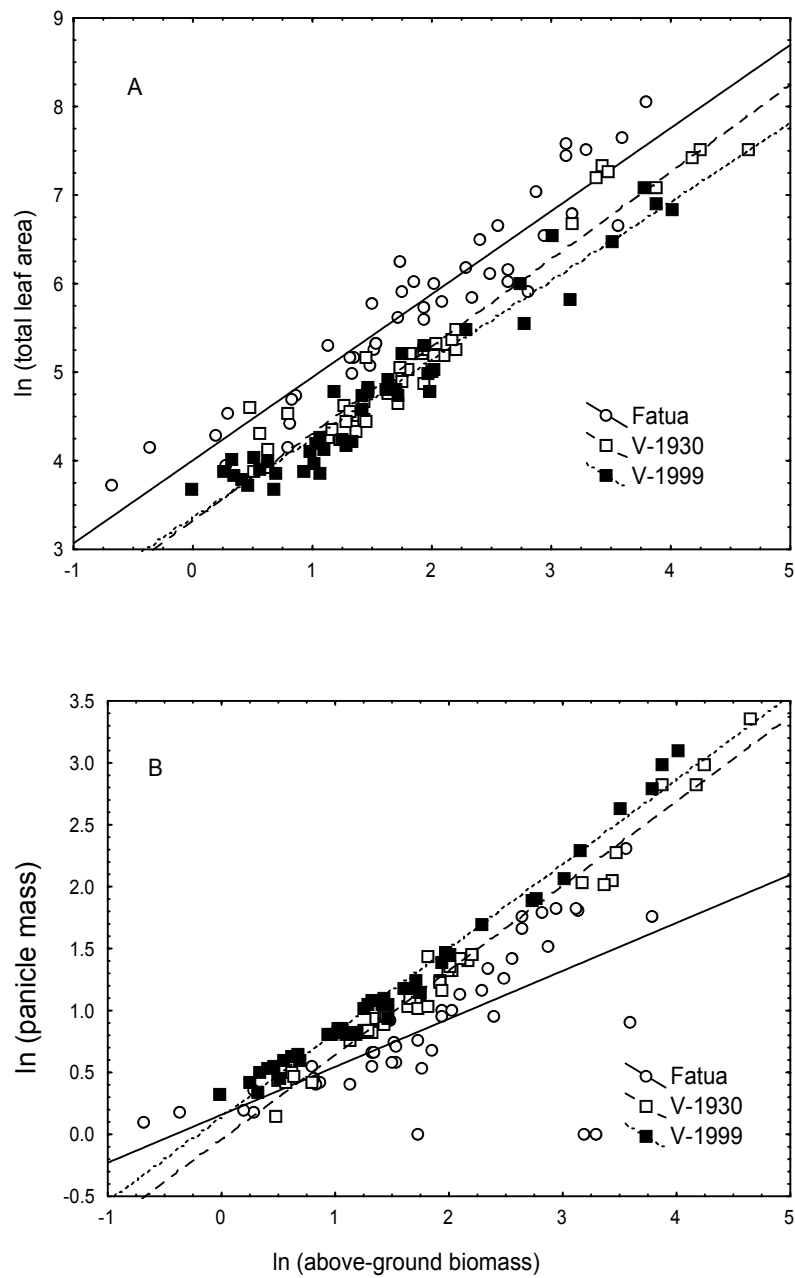
Fig. 6. Allocation to leaf area (A) and panicles (B) in two varieties of oat (*V-1930* and *V-1999*) and common wild oat (*Fatua*) under field conditions.

4. Discussion

The generally similar patterns of phenotypic plasticity in leaf area and root allocation across oat varieties and common wild oat imply that either homogenizing selection on optimal reaction norm or strong genetic/physiological constraints have prevented the patterns of plastic responses from diverging among varieties (van Tienderen, 1991; Sultan and Bazzaz 1993; De Witt, 1998; van Kleunen et al., 2000; Pigliucci, 2001; Pigliucci and Kolodynska, 2002). In other words, natural selection had enough time to test all alternative solutions to cope with varying growth conditions long before wild ancestors of today's crops were domesticated (Denison et al., 2003). Indeed, the results of this study indicate that plants are not able to perform sufficiently well under stressful conditions if changes in some traits due to passive plasticity (simple differences in growth rates) cannot provide optimal resource capture.

According to the general ontogenetic pattern detected in our study, leaf area increases, stems elongate, and allocation to roots increases and to leaves decreases (allometric slope of leaf mass (y) *vs.* root mass (x) relationship is less than 1 in log-log scale in our data) as plants become larger. But it is widely acknowledged that plants respond to shading by increasing allocation to leaf area and elongation (Sultan and Bazzaz, 1993; Stuefer and Huber, 1998; McConnaughay and Coleman, 1999; Shipley and Meziane, 2002) – responses not possible via passive plasticity, as shade-grown plants are frequently smaller than plants grown in optimal light conditions. Smaller plants are generally shorter and have less leaf area than big plants grown in sufficient light. Consequently, plants are "forced" to form slender stems (ontogenetic plasticity in stem length together with the lack of ontogenetic plasticity in stem mass) and to produce disproportionately more leaf area per given total biomass (ontogenetic plasticity in leaf area and specific leaf mass) to cope with resource shortage. Similarly, it will not be possible to increase allocation to leaves and decrease investment to roots under high-nutrient conditions via passive plasticity if the ontogenetic program dictates preferential allocation to roots. Apparently, the lack of

ontogenetic plasticity in these traits would be too deleterious for performance of crops to be unintentionally selected by plant breeders.

However, there were some differences in plasticity in leaf mass, specific leaf mass (*SLM*), and stem length among wild and cultivated oats. Obviously, some improvements in crop performance can be achieved by exploiting trade-offs between plant adaptation to natural versus agricultural conditions (Denison et al., 2003). Although wild oat examined in our study originate from agricultural landscape, it still can be considered to experience more varying growth conditions involving genetically unrelated competitors as compared to growth conditions of cultivated oats. In addition, natural selection would direct the evolution of wild oat as weed towards higher tolerance and plasticity to increase individual fitness (Baker, 1974). On the other hand, plant breeding is aimed at increasing collective performance of crops, and this is generally achieved through decrease in plant competitive ability, i.e. individual fitness. The main competitors of crop plants growing in dense stands are their congeners, given that weeds are suppressed by herbicides. Additionally, the changes in light environment during ontogeny are highly predictable, favouring passive plasticity (size-dependent changes in plant traits) over "true" adjustments in ontogeny (Bradshaw, 1965; Schlichting and Pigliucci, 1998; Alpert and Simms, 2002; Diggle, 2002; Givnish, 2002).

In the light of above-mentioned differences in selective forces involved in the evolution of wild and cultivated oats, a decrease in ontogenetic plasticity can be expected if changes in plants' growth rates due to passive plasticity will be sufficient to adjust plants' growth to given conditions so as to guarantee stable collective yield of cultivated monocultures. Differently from wild oat, cultivated oat lacked ontogenetic plasticity to light availability in allocation to leaves. Also, if wild oat produced leaves with lower mass density (*SLM*) in shade than in full daylight independent of plant biomass, i.e. exhibited pronounced ontogenetic plasticity, *SLM* of cultivated oats was largely attributable to plant's biomass, i.e. passive plasticity. As mentioned above, oats allocate preferentially to roots as plants become larger. Thus, plants will have proportionally smaller leaf mass in full sun than in shade simply due to differences in plant size. Similarly, plants have higher *SLM* in favourable light conditions simply due to larger plant size. Consequently, plants will have less leaf mass and thick leaf blades in full sun, which is consistent with the optimal growth pattern in given conditions, without employing ontogenetic plasticity.

Obviously, wild oat needs pronounced plasticity in leaf mass and *SLM* to cope with variable conditions characteristic of their growth habitats, but cultivated oat is selected for a fixed development that can produce high collective yield in stable conditions.

We observed a decrease in ontogenetic plasticity in stem length as the consequence of breeding in oats. Plant height and its plasticity are known to be very important in plant competition for light (Givnish, 1982; Weiner and Thomas, 1992; Ballaré and Scopel, 1997; Schmitt, 1997; Westoby et al., 2002; Falster and Westoby, 2003). Still the reduction in plant height has been a major source of crop yield improvement during the last few decades (so called "Green Revolution"; Evans and Fischer, 1999; Peng et al., 2000; Denison et al., 2003; Weiner, 2003; Vandeleur and Gill, 2004). However, changes in crop's plasticity in vertical growth in response to competition for light have rarely been addressed (Didon, 2002). Additionally, even if changes in crop's morphology in response to competition with weeds were examined, these changes were indicated as the competitive response of the crop without discriminating between passive and ontogenetic plasticity. In agriculture, there is the established opinion of competitive response being deleterious to crops and suppressive effect being positive in selection for competitive varieties (Lemerle et al., 1996; Johnson et al., 1998; Seavers and Wright, 1999; Didon, 2002). However, from ecologist's point of view, passive plasticity is a maladaptive response to competition, whereas ontogenetic plasticity of plants can have a pronounced *effect* on their competitors being at the same time a competitive *response* to the very same competitors. For example, elongation of stems is a response to competition which may reduce crop yield due to increased allocation to vertical growth, but can preclude shading by weeds (via competitive effect on weeds) and, thus, avoid even larger losses in the yield.

The appropriateness of plasticity in stem elongation in cultivated oats seems to depend on the argotechnology in use. In case of wild oat, plasticity would be favoured by natural selection as plants have to compete for light in various competitive conditions. Indeed, wild oat exhibited very high plasticity in stem elongation in the pot experiment as well as grown in the field (Fig. 2, 4). As has been mentioned above, the situation is completely different for cultivated oats. Due to herbicide use, the main competitors of oats are their congeners, and due to inbreeding plant individuals are very similar to each other, and are obviously unable to overtop their competitors. It is

acknowledged that if the chances to escape shading by competitors are restricted, the elongation response will become too costly as a result of an increased carbon allocation to supportive tissues and reduced mechanical stability (Dudley and Schmitt, 1996; Steinger et al., 2003; Weinig, 2000a, b; Weinig and Delph, 2001). At this point, the decreased plasticity of V-1999 should have advantageous effects on plant reproductive fitness and overall population productivity.

We observed decreased plasticity in stem length in the modern variety as compared to older varieties and wild oat. The clearly non-linear reaction norms of stem length to light in cultivated oats (Fig. 1B in I) indicate that plants achieve maximum stem length at some intermediate light intensity, above which it is more appropriate to invest biomass into other functions than elongation. It is likely that shade-tolerant plants should cease to elongate at lower light intensity and consequently produce relatively shorter stems in full light than light-demanding plants. Different varieties demonstrated contrasting behaviour here, best illustrated by comparing V-1952 and V-1999. Evidently, the negligible difference in stem length between moderate shade and full daylight treatments, and thus greater susceptibility to shading, observed in V-1999, is the direct consequence of a strongly biomass(size)-determined stem elongation and can be considered to be a by-product of decreased plasticity. The observation that V-1999 produced the shortest stems in 10% light, where extensive stem elongation per given biomass is needed, also indicates susceptibility to shade in the modern variety. In contrast, the stem length of V-1952 plants was almost independent of total biomass (Table 1 in I) and showed a clear difference between 50% and 100% daylight treatments, implying high plasticity in elongation. A possible increase in susceptibility to low light as a result of decreased plasticity to light quality (crowding) has been discussed already by Ballaré et al. (1994). Our results provide indirect evidence that this could be true in the oat varieties under examination.

However, considering the current concerns about herbicide usage, the competitive abilities of crops are likely to become valued again (Christensen, 1994; Lemerle et al., 1996; Cousens and Mokhtari, 1998; Johnson et al., 1998; Seavers and Wright, 1999; Weiner et al., 2001; Vandeleur and Gill, 2004). In this respect, varieties with the greatest ontogenetic plasticity in stem elongation should be favoured in breeding. The most appropriate variety for further selection could be V-1952, the variety that has been released at times of limited weed control.

It is unknown, however, whether the decreased plasticity of stem elongation in response to light intensity, found in our study, is accompanied by a reduced sensitivity to light quality. The field study has shown that V-1999 exhibited some stem elongation in response to high sowing densities and to competition with V-1930 in early stages of development, but was not able to maintain sufficiently high rates of elongation until the end of the experiment. Consequently, although having shown some elongation response early in the season, V-1999 was overtopped by the older variety by the end of the experiment. Due to stem elongation being highly biomass-dependent, V-1999 was unable to adjust its development to succeed in the competition with the genetically different competitor. Due to greater susceptibility to shading indicated in the pot experiment, plants of V-1999 had eventually even shorter stems than in monocultures of the same density, a response that is maladaptive in the competition with more plastic V-1930. The lack of plasticity in elongation in V-1999 resulted in reduced biomass and panicle production as compared to V-1930. However, V-1999 performed equally well with V-1930 when grown in monocultures where competitors are genetically similar, and all plants lack plasticity in elongation. To support the idea of importance of plasticity in competition between the two varieties, it should be mentioned that the observed differences in performances of the two varieties cannot be attributed to mortality of plants during the experiment, different growth potentials or light interception abilities. In addition, given the same above- and below-ground space and resource amounts in the pot experiment, V-1999 had equal or even taller stems than V-1930 under the range of resource levels that implies no inherent differences in plant height between the two varieties.

The extraordinary ability of wild oat to occupy space and tolerate shading is clearly seen in our study. In spite of poor germination and small seed mass, wild oat was able to fully exploit available space and produce closed canopies that intercepted as much light as densely sown cultivated oats. This was mainly achieved by extensive plasticity in tillering: few tillers in dense mixtures and many-fold increased tillering in sparse monocultures and single-grown plants (Fig. 3). In addition, wild oat produced significantly more leaf area per given biomass than cultivated oats. Irrespective of small seed size and consequent slow seedling establishment (little biomass at the first sampling), wild oat was able to take an advantage of abundant light once established and multiply its growth rate to produce as much biomass per unit land area in monocultures as cultivated oats. Moreover, it was even able to slightly overtop plants

of V-1999 in the mixed stands that resulted in higher biomass production and seed output in the mixture with V-1999 as compared to growth in the mixture with V-1930. Good performance of wild oat in dense mixtures may be primarily attributed to great ontogenetic plasticity in stem length. It was able to tolerate early shading by large-seeded cultivated oats in the beginning of the experiment, and to produce strongly elongated stems per given biomass that resulted in attainment of equal shoot heights with its competitors.

The results of our study show that plant breeding has caused major changes in plant's growth strategy. Wild oats are known as one of the most competitive of the annual grass weeds (Medd, 1996). However, little information is available on the competitive differences between crop cultivars and wild oats (Nietschke, 1996). May be that is why agriculturists often think of weeds as highly successful plants that have the ability to strongly suppress the growth of crops (Baker, 1974). On the contrary, weedy species are not often the most successful when judged by the evolutionary criteria. Usually weeds are opportunists which are restricted in their distribution in native habitats and become locally abundant in areas of human disturbance (Palmblad, 1968; Baker, 1974). A considerable part of known weed species, *A. fatua* included, exhibit such "ideal weed" characteristics as stress tolerance, production of seeds in a wide range of environmental conditions, and high plasticity (Baker, 1974). Variable seed output, small seed size, slow seedling establishment, tolerance of early shade in the mixtures with cultivated oats, persistent stem elongation via ontogenetic plasticity, and greater allocation to leaf area define common wild oat rather as a species having features of "SC-strategy" (stress-tolerant and competitive), not an aggressive weed severely suppressing crop growth. On the contrary, fixed progressive allocation to reproduction and shortened vegetative growth in modern oat varieties imply that, in the language of life history theory, selection for improved yield potential has resulted in crops being "R-strategists" (Begon et al., 1996; Pigliucci, 2001; Weiner, 2003). Reduced plasticity in several traits and consequent decline in the competitive ability of cultivated oats as well as high initial growth rate of the modern oat variety also support the idea of modern crops becoming "R-strategists". The oldest oat variety examined in our study can be viewed as an intermediate strategist that has partially reduced plasticity in comparison to wild oat, but still has strong competitive effect thanks to its tall stature and greater allocation to vegetative growth.

Summary

New directions in crop improvement via alteration of plant responsiveness to variation in growth conditions are being actively debated. It appears, however, that little is known about the impact of previous breeding on the phenotypic plasticity of plants, which results from correlated responses to selection on high yield.

We used four oat (*Avena sativa* L.) varieties, originating from 1930, 1952, 1980 and 1999, to examine the effects of long-term breeding on the patterns of autecological phenotypic responses to variation in light and nutrient supply. Phenotypic plasticity of common wild oat (*Avena fatua* L.) and its interactions with the oldest (originating from 1930) and the youngest available oat varieties (originating from 1999) were also examined to compare cultivated oats with their wild ancestor.

Our results support the idea that, in conditions of present-day agronomy, it can be more advantageous in the breeding of crop plants to select for a fixed pattern of allocation to different tissues, dependent on developmental stage, than to select for the ability to adjust the whole ontogeny to particular environmental conditions. Obviously, it is not possible to lose ontogenetic plasticity, as such, entirely: plants will have to adjust their development in response to stressful conditions if the allocational pattern of underdeveloped plants is not consistent with optimal foraging behaviour. The similar patterns of plastic responses in some traits of the studied oat varieties and common wild oat imply that either homogenizing selection on optimal reaction norm or genetic constraints have prevented oats from further evolution.

Field trials showed that high yield potential of the modern variety may be associated with improvements in collective performance of crop monocultures via reduced competition for light among individual plants (lack of plasticity in stem elongation). However, the positive effect of reduced plasticity on yield was repealed when the modern variety experienced a different competitive environment. Modern oats were unable to adjust their vertical growth to succeed in competition for light with genetically different and plastic plants of the old variety.

Cultivated oats had initial advantage in growth over wild oat due to their larger seed size and consequent better seedling establishment. However, wild oat was able to produce dense canopies in monocultures and reach equal shoot heights with the old oat variety and even overtop the modern variety by the end of the experiment. Obviously, good performance of wild oat may be attributed to its pronounced plasticity in tillering and stem elongation.

Variable reproductive allocation, small seed size, high plasticity and shade tolerance define wild oat as "SC-strategist". On the contrary, fixed development, preferred allocation to reproduction, and shortened vegetative growth of the modern oat variety shows that breeding for high yield has resulted in crops becoming "R-strategists".

Kokkuvõte

Uue põllukultuuride aretussuunana on viimasel ajal käsitletud taimede reageerimisvõime muutmist vastusena kasvutingimuste varieeruvusele. Samas on tänase seisuga vähe teada eelneva aretustöö kaudsest mõjust taimede fenotüübilisele plastilisusele, mis kaasneb otsese valikuga kõrge saagipotentsiaali suunas.

Käesoleva uurimistöö raames kasutasin nelja eri aastatest (1930, 1952, 1980, 1999) pärinevat kaerasorti (*Avena sativa* L.), et uurida pikaajalise aretuse mõju taime eri tunnuste reaktsiooninormidele vastusena valguse ja toitainete kättesaadavuse varieeruvusele. Võrdlemaks kultiveeritud kaera tema loodusliku eellasega hindasin lisaks tuulekaera (*Avena fatua* L.) plastilisust valguse kättesaadavuse suhtes. Samuti uurisin tuulekaera ja kahe kultiveeritud sordi (1930, 1999) vahelisi interaktsioone põllutingimustes.

Eksperimendi tulemused toetavad oletust, et kaasaegse agrotehnika tingimustes on aretuses kasulikum selekteerida kindla fikseeritud biomassi allokatsioonimustri suunas, mis sõltub ainult taime arengustaadiumist, mitte aga paindliku kasvutingimuste muutustele reageeriva ontogeneesi suunas. Ilmselgelt ei saa taimed kaotada plastilisust kui sellist täielikult: taim on sunnitud korraldama oma ontogeneesi ümber vastusena stressile juhul kui alaarenenud taimede biomassi allokatsioonimuster ei vasta antud tingimustes optimaalsele ressursside omastamise strateegiale. Uuritud kaerasortide ja tuulekaera sarnased reaktsiooninormid mõnede tunnuste osas viitavad tasakaalustavale valikule optimaalse reaktsiooninormi suunas ja/või geneetilistele piirangutele, mis takistavad plastilisuse edasist evolutsiooni.

Põllukatse demonstreeris, et kaasaegse sordi kõrge saagipotentsiaal võib olla seotud populatsiooni tootluse suurenemisega kaera monokultuurides läbi isenditevahelise valguskonkurentsi vähenemise (vähene plastilisus varre pikkuses). Kuid kahanenud plastilisuse eelis kadus kui kaasaegne sort kasvas aretamise keskkonnast erinevates konkurentsitingimustes. Kaasaegse sordi taimed polnud võimelised kohandama oma vertikaalset kasvu, et olla edukad valguskonkurentsis geneetiliselt erineva ja plastilise vana kaerasordiga.

Kaerasordid omasid algset kasvueelist tuulekaera ees tänu kaeraseemne suuremale kaalule ja sellest tulenevavale kiiremale seemikute kohanemisele. Vaatamata sellele oli eksperimendi lõpuks tuulekaer võimeline moodustama monokultuurides sama tihedaid võrasid kui kaerasordid, saavutama vana kaerasordiga võrdset taimekõrgust ja isegi kasvama kaasaegsest sordist üle. Tuulekaera hea kasvusuutlikkus on ilmselt seotud tema kõrge plastilisusega võsude arvus ja varre pikkuses vastusena konkurentsile.

Varieeruvus allokatsioonis õisikutesse, väike seemne suurus, kõrge plastilisus ja varjutaluvus iseloomustavad tuulekaera kui „SC-strateegi". Samas kaasaegse kaerasordi eelistatud allokatsioon reproduktsiooni, lühenenud vegetatiivne kasv ja kahanenud plastilisus näitavad, et aretuse tagajärjel on kaer muutumas hoopis „R-strateegiks" ehk ruderaaliks.

Acknowledgements

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