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INTERACTIONS BETWEEN <u>PHRAGMITES</u> AUSTRALIS (CAV.) TRIN. EX STEUD. AND TYPHA LATIFOLIA L.*

ABSTRACT: In experimental conditions the interactions between Phragmites australis and Typha latifolia were analysed. In mixed cultures with the reed the cattail gained biomass, whereas the reed lost.

KEY WORDS: Phragmites, Typha, competition, crowding, density, interactions, interference.

Contents

1. Introduction

2. Material and methods

3. Results

3.1. Growth rate

3.2. Shoot height

3.3. Shoot weight

3.4. Number of shoots

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3.6. Production per pot

- 4. Discussion
- 5. Conclusions
- 6. Summary
- 7. Polish summary
- 8. References

1. INTRODUCTION

The interactions between terrestrial plant species have been dealt with in quite a number of papers (M o l i s c h 1937, K n a p p 1960, B ö r n e r 1968, G r o d z i n' s k i j 1973, R i c e 1974), while aquatic and marsh plants have received little attention.

The tendency seen in macrophytes to form large monospecific stands suggests that these plants possess some mechanisms which prevent, or at least limit the occurrence of other macrophyte species, thereby favouring monospecific assemblages. These observations contradict D a r w i n's (1959) statement that the fiercests struggle for survival occurs among the individuals of the same species, because their requirements are almost identical and their adaptations to this struggle are most similar. In his discussion on the state of investigations into the competition of higher plants Z ar z y c k i (1965) argues Darwin's statement by saying that intraspecific competition is not always stronger. Individuals and species do not only compete with one another; their interactions are sometimes positive in nature.

It is necessary to clarify the role of inter- and intraspecific interactions to be able to correctly interpret the distribution of plants - in this case the macrophytes - and assess the processes of succession.

In the field, the finding of interactions is made difficult by the presence of many biotic factors and their great diversity. In an experiment where conditions are maintained at a level as even as possible, it is easier to identify such relationships. It was for this reason that culture experiments were undertaken to determine the interrelationships between <u>Phragmites australis</u> and <u>Typha lati-</u> <u>folia</u>. The final result expressed in the condition and production of the plants was analysed as the resultant of the two types of interactions.

2. MATERIAL AND METHODS

In the years 1970 and 1977, plants were grown in an open area in 5-litre plastic pots filled with profundal mud from the Mikołajskie Lake, similarly to other experiments (S z c z e p a ń s k i 1978). Each pot contained 4.5 l of mud. During the culture the plants were watered with unchlorinated tap water, water being applied in sufficient quantity to maintain a thin water layer above the mud. From germinating beds consisting of mud with reed and cattail seeds planted in it separately, the seedlings were transferred to 5-litre pots. In these pots different proportions of seedlings were planted (Table I). In 1970, the experiment consisted of 11 variants, in 1977 - of 3 variants.

mar or the fee	Initial number of individuals													
Species	1970									1977				
Phragmites australis	10	9	8	7	6	5	4	3	2	1	0	10	5	0
<u>Typha</u> <u>latifolia</u>	0	1	2	3	4	5	6	7	8	9	10	0	5	10

Table I. Scheme of the experimental series of 1970 and 1977

In 1970, the culture experiment started on 10 April and terminated on 28 August. In 1977, the culture was started on 17 June and terminated on 21 September. In 1970, the culture lasted 140 days. in 1977 - 96 days. In 1970, the transplanted reed and cattail seedlings were 3-4 cm tall, and in 1977 the reed seedlings were 14 cm, and the cattail seedlings 8.5 cm tall. In 1970, the plants were measured and counted every month, and in 1977 every two weeks. At the termination of a culture the aboveground parts were cut down at the surface of the mud. For determining the dry weight, the aboveground parts and the underground parts, previously washed, were dried at 105°C to a constant weight.

The analysis of the material of 1970 was based on mean values from 3 replications, and that of 1977 on mean values from 5 replications.

In both years the average weight was calculated of one shoot, the average biomass of the particular species per pot, as well as the number and biomass of the shoots produced by one seedling. In each pot the tallest shoot was measured, and for each variant the maximum mean was calculated, whereas at the termination the mean was additionally calculated from 3 tallest shoots in each pot.

For each year the control adopted for the particular species consisted of the height of a plant, weight of one shoot, the number of shoots produced, production per pot and the production of one seedling of the species grown in a monoculture at the density of 10 individuals per pot. All the above features described the condition of a plant. The adoption of the condition of particular plant species grown in a monoculture of initial density of 10 individuals per pot as a control was justified by the fact that all the mixed culture versions had 10 seedlings per pot. An increase in density affects the condition of a plant (Y o d a et al. 1963, R i s s e r 1969, S z c z e p a ń s k a and S z c z e p a ńs k i 1976). When considering the interactions between different plant species, a uniform, summarized density should be adopted for the whole culture.

As the condition of plants in the corresponding versions in the two culture years was different (because the beginning of the culture, the climatic conditions and the culture time were dif-

ferent), the numerical data obtained had to be converted to percentages in relation to the control for the particular year. The control was adopted as 100%.

3. RESULTS

3.1. Growth rate

The course of the growth of the two plant species under study is typical of herbaceous plants, i.e., an intensive growth in height in the first half of the growing season is followed by a decrease in the growth rate, to reach zero point in September. The differentiation of the growth rate in fact begins from the moment the seedlings are planted in pots (Fig. 1). In the monoculture the reed showed the highest growth rate. This rate dropped proportionately to the increase of the proportion of the cattail in the mixed populations.

During the most intensive growth, at the turn of May 1970, the height increment amounted to 6.3 mm a day in the monoculture, 3.7 mm



Fig. 1. Growth rate of Phragmites australis in 1970 - monoculture, 2 - 5 seedlings of Phragmites + 5 seedlings of Typha, 3 - 1 seedling of Phragmites + 9 seedlings of Typha a day in the mixed populations (5 reed and 5 cattail seedlings) and only 1.9 mm a day in a culture where the reed represented only 10% of the population.

On the termination of the experiment on 28 Aug. 1970, the height of the reed in the monoculture was 66.1 cm, in the variant with the cattail (5 reed : 5 cattail individuals) - 46.1 cm, and in the variant with 1 reed seedling per 9 cattail seedlings the height of the reed came up to 32.7 cm. Thus in the monoculture the reed was more than twice as tall as the reed in the mixed population with the cattail - 1 reed per 9 cattail seedlings.

The cattail did not respond by changing the growth rate to the presence of the reed in culture (Fig. 2). In fact the growth rate



Fig. 2. Growth rate of Typha latifolia in 1970

 monoculture, 2 - 5 seedlings of Typha + 5 seedlings of Phragmites, 3 - 1 seedling of Typha + 9 seedlings of Phragmites

curves in the particular variants overlap. Under the conditions of this experiment the cattail attained a height of 52.9 cm in the monoculture, and slightly more in the mixed variants.

The nature of the growth rate curve of the cattail is the same as that of the growth rate curve of the reed.

In the experiment of 1977 the differences between the monoculture and the mixed culture were not as great as in the experiment of 1970,



Fig. 3. Growth rate of Phragmites australis in 1977 1 - monoculture, 2 - 5 seedlings of Phragmites + 5 seedlings of Typha

probably because the culture was started at a later date and the culture time was shorter, though in the last case, too, the reed in the monoculture was clearly taller (Fig. 3).

3.2. Shoot height

The height appears to be the most conservative feature of the condition of the plants studied. It is, therefore, least prone of changes due to the experimental conditions. But even in this case it is possible to follow the reaction.

The reed showed a directly proportionate relationship to the number of seedlings in a pot (Fig. 4). This relationship, y == 3.27 x + 25.33 significant at the level of 0.001 (r = 0.96), disagrees with data on the relationship between the plant condition and density (H o l l i d a y 1960, Y o d a et al. 1963, R i s s e r 1969, H a r p e r and W h i t e 1974, S z c z ep a ń s k a and S z c z e p a ń s k i 1976), which makes it possible to presume that the growth in height of the reed in pots



Fig. 4. Relationship between the height and density in 1970 - Phragmites: y = 3.27 x + 25.33; r = 0.96; 2 - Typha: y = 0.86 x + 44.17; r = 0.67

with an increasing number of reed seedlings depended on the decreasing density of the cattail. With the decreasing number of cattail seedlings the negative effect of the cattail on the reed decreased, this being the cause of the observed growth in height of the reed.

The cattail responded to changes in the number of reed seedlings by a much weaker change in height - y = 0.86 x + 44.17, with a much lower correlation coefficient.

In the experiment of 1977, regression could not be determined, because of the scheme of the experiment. It was only possible to establish changes in height caused by the mixed culture. Also in this experiment the reed slowed down its growth in response to the presence of the cattail. Its growth rate in the mixed culture (5 reed + 5 cattail individuals) was lower and represented 88.6% of the growth rate in the monoculture. In 1970, the respective quantity was 66.8%.

In the experiment of 1977 the cattail in the mixed culture was shorter than in the monoculture, while in 1970 it was taller.

3.3. Shoot weight

Reed shoot weight increased with the growth of the proportion of the reed in the mixed population (Fig. 5) from 0.080 g in the



Fig. 5. Relationship between the dry weight of shoots and density 1 - Phragmites, 2 - Typha

combination consisting of 1 reed seedling and 9 cattail seedlings to 0.179 g in the monoculture, with a fairly high correlation coefficient (r = 0.82) at the level of significance below 0.01. The weight of a cattail shoot at first decreased rather quickly and then remained at a relatively stable level, but in this case also the correlation coefficient was 0.77 at the level of significance below 0.01.

In the experiment of 1970 the weight of a reed shoot from the mixed culture represented 69.1% of the weight of a shoot from the monoculture, and in the experiment of 1977 the respective quantity represented 81.1%. In 1970, the weight of a cattail shoot was 112.0% relative to the monoculture, and in 1977 - 113.1%.

Both experiments indicate that when grown in a monoculture, the reed produces heavier shoots, while the cattail produces heavier shoots in a mixed culture.

3.4. Number of shoots

The number of shoots produced by a seedling in the experiment of 1970 appeared to be fairly even, not fully reflecting the directional variation of the experiment. For the reed it amounted on the average to 3.5 shoots per seedling (Fig. 6). The cattail pro-



Fig. 6. Relationship between the number of shoots produced by one seedling and density 1 - Phragmites, 2 - Typha

duced fewer shoots, only 1.5 shoots per seedling, this quantity being very uniform (Fig. 6). In this case, too, the largest number of shoots produced by a reed seedling was recorded for the monoculture (4.3 shoots, the average being 3.5), while the number of cattail shoots produced in the monoculture was smaller (1.3, the average being 1.5).

In 1977, the production of shoots by a reed seedling in the monoculture amounted to 4.5 shoots, and in the mixed culture to 3.7 shoots. A cattail seedling in the monoculture, as in the mixed culture, produced 1.1 shoots.

It is possible that in the growing season of 1977 there existed conditions more favourable for the growth of the reed and hence the larger number of shoots produced.

3.5. Quantity produced by one seedling

The dry weight produced by one seedling is the total of the weights of shoots formed during a growing season. This quantity

most clearly reflects the effect of factors limiting, or stimulating the growth of plants.

In the case of the reed, the production of a seedling in the mixed culture was lower than in the monoculture and amounted in 1970 to 57.4%, and in 1977 to 72.2% of the value for the monoculture. Under the same conditions the cattail showed a higher production in the mixed culture than in the monoculture. The corresponding values were 129.8% in 1970 and 115.1% in 1977.

In the experiment of 1970 the biomass produced by a reed seedling grew in a manner directly proportionate to the number of reed seedlings in a pot. Because of a fairly great dispersion, the correlation coefficient amounted to 0.47 (t > 0.2) (Fig. 7). The pro-





duction of a cattail seedling appeared to be inversely proportionate to the number of cattail seedlings in a pot, while the correlation coefficient was very high (-0.96 at t > 0.001).

3.6. Production per pot

Regardless of the numerical ratios of the seedlings, the final value of production per pot varies over a fairly narrow range. It

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Fig. 8. Aboveground biomass per pot 1 - Phragmites, 2 - Typha

varied between 7.67 g per pot and 9.55 g per pot, the average being 8.49 g per pot (Fig. 8). The straight line of regression was y = -0.114 + 9.0554.

As indicated by the equation, its fall is very slight. One could really speak of equalized values of the joint biomass production, regardless of the initial composition of the seedlings. In the experiment of 1977 the reed in the monoculture produced 5.55 g per pot, a cattail-reed mixture - 4.57 g per pot, whereas the cattail in the monoculture 4.45 g per pot. Also in this experiment the quantities were fairly similar, although a reed shoot weighed 0.124 g, and a cattail shoot - 0.404 g.

A similar situation, though at a higher level, was found in respective values for underground organs (Fig. 9). The average was 12.43 g per pot and varied between 10.96 g per pot and 13.45 g per pot. The straight line of regression equals y = 0.0041 x + 12.45. This is, therefore, a horizontal line indicating that the biomass produced in a pot did not depend on the initial composition of the seedlings in a pot. As could be expected, the total biomass of the aboveground and the underground parts produced in one pot gave the



Fig. 9. Total biomass of Phragmites and Typha per pot A - aboveground biomass, B - underground biomass, C - total biomass

same picture. The average for the whole experiment of 1970 was equal to 20.92 g per pot, ranging from 18.63 g per pot to 22.65 g per pot. The indices of variation of the means were 7.9% for the aboveground parts, 10.1% for the underground parts and 5.3% for the total biomass produced in a pot, being thus fairly low, which indicates that the data are equalized.

4. DISCUSSION

In a mixed culture it is difficult to separate elements of intraspecific competition from elements of interspecific competition. The picture obtained is the resultant of the two actions, and if the behaviour of a species in a mixed culture is different from that in a monoculture, it may be presumed that this is the result of the overlapping of interspecific and intraspecific actions, bearing it in mind that the response results from the two types of interaction.

The relationship between the density of sowing and the yield has long been the object of interest of farmers and gardeners (Gieseke 1954). Kira, Ogawa and Sakazaki (1953) have suggested a competition-density effect law as a crude approximation of the effect of density upon plant growth. The competition-density law has consistently been extended, and in 1956 the logistic theory of the C-D effect was developed (Shinozaki and Kira 1956).

Harper and White (1974) have distinguished three stages in the development of a population in a constant capacity of an environment. Stage I of exponential growth, Stage II of linear growth and Stage III of equilibrium - when increment is counterbalanced by losses. On account of the assumptions made and the duration, our experiments covered only the first two stages. In experiments with helophytes Stage III is attained in the next growing seasons only.

As stressed by S o l b r i g (1980), the generalized conclusions of K i r a, O g a w a and S a k a z a k i (1953) and of other investigators apply primarily to monospecific populations. Interspecific interactions have been studied chiefly by agrobiologists, but mainly with regard to agricultural productivity. In his paper "On competition" D e W i t (1960) has presented some theoretical principles of interspecific interactions. H a l l (1974) has developed D e W i t's (1960) approach mainly by analysing the factors for which plants compete.

The crowding coefficient worked out by D e W i t (1960) takes values from $+\infty$ to $-\infty$, the jump (change of sign) occurring when the value of the yield in a mixed culture is equal to the value of the yield in a monoculture. Accepting D e W i t's (1960) concept, we have used a simpler interaction coefficient: K = $\frac{C \cdot 100\%}{M \cdot P}$ where: K - competition coefficient, M - yield in monoculture at a specified density, C - yield of a species in mixed culture, P index of proportions of sowing of a species in mixed culture.

The analysis of competition according to D e W i t (1960) assumes that at least 3 numbers can be obtained. The value of the yield of two species in monocultures and of the yield of a parti-

Interactions between Phragmites and Typha

cular species from a mixed culture of known sowing proportions. D e W i t (1960) suggests sowing of a mixed culture in several proportions and calculating the crowding coefficient for each proportion and averaging this coefficient. In the cultures used as the basis for conclusions D e W i t (1960) used mixtures in which the species under study represented 0.33, 0.5 and 0.67 of the number of seeds sown.

In the experiment of 1970, 9 mixed culture variants and 2 monocultures were used. Data from the experiment of 1970 (Fig. 10) indicate that the biomass of the reed was lower than could be expected from its initial positions. The cattail grown in a mixed culture produced more biomass per pot than the biomass quantity calculated from the monoculture and the percentage in mixed culture. Since these two plants differ in their biomass, to increase the comparability, relative biomass values have been computed representing the production of both species in per cent, relative to their monocultures. In this way the difficulty can be overcome of comparing different biomasses (Fig. 11). This procedure is recom-



Fig. 10. Production of Phragmites and Typha growing in a mixed population of different proportions
A - Phragmites - solid lines, B - Typha - dashed lines. Straight line - theoretical production resulting from proportionality, broken line - real production



Fig. 11. Changes of production of Phragmites and Typha growing in mixed populations of different proportions
A - hatched area - reduction in production of Phragmites, B hatched area - increase of production of Typha

mendable especially when monocultures differ rather significantly. The hatched areas in Figure 11 represent a reduction in the production of the reed and an increase in the production of the cattail, relative to their hypothetical production if there had not been any interference.

The competition coefficient $K = \frac{C \cdot 100\%}{M \cdot P}$ calculated for this experiment tends towards 100%, for the two species from opposite positions (Table II).

Table II. Changes of the coefficient of competition in relation to the initial proportion of the particular species in mixed culture

Species	Proportion of species in pot in per cent										
	10	20	30	40	50	60	70	80	90	100	
Phragmites australis	41.7	45.0	36.1	47.9	57.6	48.0	59.6	35.9	75.8	100	
<u>Typha</u> <u>latifolia</u>	450	319	182	161	130	120	134	114	115	100	

The competition coefficient of the reed remained at the level of 40-60% for a long time, and only in the variant with 1 cattail and 9 reed seedlings did it rise to 76%. But the same coefficient for the cattail was at the beginning 450% (1 cattail + 9 reed seedlings) and then fell down to a hundred and a dozen per cent, whereafter it grew gradually to 100% in the monoculture.

In this experiment the reed is the species that clearly loses in the competition with the cattail which clearly wins. Noteworthy is the fact that in the variant including 1 cattail and 9 reed seedlings the reed loses least (25%) and the cattail gains most (450%). The competition coefficient calculated in the experiment of 1977 for the variant with 5 reed and 5 cattail individuals equals 72.3% for the reed and 115.1% for the cattail. Thus the interference was in that year slightly weaker for the cattail. (For 1970, these values for the corresponding culture variants were: 57.6% the reed and 130% - the cattail.)

K n a p p (1960) has found that the type of substrate may be one of the factors revealing, or not revealing allelopathic influences. Mixed cultures of the reed and the cattail on different substrates in 1969 (S z c z e p a ń s k a 1971) have shown that on garden soil the biomass produced by one reed seedling is lower by 67% relative to the reed biomass in monoculture, while the biomass of the cattail in a mixed culture with the reed is higher by 75%. Grown on lake mud, the reed in a mixed culture with the cattail produces 61% less biomass than in a monoculture. The cattail grown in mixed populations with the reed produces 40% more biomass than in a monoculture. As we have seen, the substrate is a factor to a considerable degree determining the magnitude of the interspecific influences.

Furthermore, the magnitude of the interspecific interactions varies from year to year, this being probably connected with the different culture times and weather conditions. This may result from the fact that competition develops with the development of plants, and in 1977 the culture experiment lasted much shorter than in 1970. Regardless of the changes in the production of the individual species, the total biomass in a pot was not subject to any greater variations (Fig. 9), and it may be stated that the total biomass is a measure of the capacity of a habitat.

Analyses of the material show that the production per one seedling of the reed was fairly uniform and equal to ≈ 0.36 g per pot, and only in the variant with 1 cattail + 9 reed individuals it increased to 0.58 g. and in the monoculture up to 0.77 g. Cattail production per seedling was inversely proportionate to the density of seedlings. Thus the cattail's response to its own density was negative, while the reed reacted positively to its own density. The above finding contradicts the data from earlier studies (Szczepańska and Szczepański 1976). However, this is only a seeming contradiction. In the mixed culture the growth of the reed was suppressed by the cattail with a force proportionate to the number of cattail seedlings in the mixed culture. The impeding effect of the cattail decreased as the number of its seedlings in the mixed culture diminished, whereas the impeding effect of the reed, which increased with the growth of density. was lower by as much as not to counterbalance the decreasing negative effect of the cattail. As a result, an increased reed production was observed. The interferences of both species were realized by changes in the value of the production by one seedling (Fig. 7), but the number of shoots produced by one seedling was relatively stable (Fig. 6). The weight of one shoot varied, and it varied in both species differently (Fig. 5). In the reed. the shoot weight increased as the number of interfering cattail individuals decreased, and as the proportion of the reed in the culture increased. Grown in pots with a small number of its own individuals, the cattail had characteristically higher shoot weight. whereas at higher densities its shoot weight remained at the same level. This growth in weight appeared to be correlated with the growth in height (Fig. 4) which was in the reed 4 times stronger.

5. CONCLUSIONS

1. When grown in mixed cultures, helophyte species act upon each other. This interaction may result in (a) a deterioratica of the condition of the plants, thereby a lower production, or (b) an improvement of the condition, thereby a higher production, or (c) a species behaves as if it did not react to the presence of another species. The reed clearly reacted according to (a), but the cattail partially according to (b) and partially according to (c).

2. Under the conditions of the experiment, the plants reacted principally by changes in the shoot condition, and to a lesser extent through a reduction in the number of shoots produced.

3. Interacting species are at the same time subject to the density effect. This crowding-density effect is superimposed on the interference, and may dominate over it (cattail), or may be dominated by it (reed).

In nature, in addition to the above-enumerated relationships there are other biotic and habitat factors, and it is the whole of these relationships that is responsible for the physiognomy of plants.

6. SUMMARY

In the years 1970 and 1977, experiments were carried out on a mixed culture of two helophyte species - <u>Phragmites australis</u> and <u>Typha latifolia</u>. The interactions between these plants were determined on the basis of growth and production characteristics.

Analyses were carried out of: growth rate (Figs. 1-3), shoot height (Fig. 4) and weight (Fig. 5), and number of shoots (Fig. 6), production by one seedling (Fig. 7), production per pot (Figs. 8, 9).

To demonstrate the interactions, a competition coefficient has been worked out: $K = \frac{C \cdot 100\%}{M \cdot P}$ (C - the yield of the species under study in a mixed population, M - the yield obtained in monocultures at a specified density, P - coefficient of sowing proportions of the species studied in mixed populations). This coefficient has shown that when grown in a mixed culture, Typha latifolia gains in weight relative to a monoculture, while Phragmites australis loses (Figs. 10, 11).

Changes in biomass were effected mainly via changes in the condition of the shoots, and to a lesser extent through changes in the number of shoots formed.

7. POLISH SUMMARY

W latach 1970 i 1977 prowadzono eksperymenty nad wspólną hodowlą 2 gatunków helofitów - Phragmites australis i Typha latifolia. Określano wzajemne wpływy tych roślin oceniane na podstawie charakterystyk wzrostu i produkcji.

Analizowano: tempo wzrostu (rys. 1-3), wysokość pędów (rys. 4), ich masę (rys. 5) i liczbę (rys. 6), produkcję wytworzoną przez jedną sadzonkę (rys. 7), produkcję na naczynie (rys. 8-9).

Dla unaocznienia wzajemnych oddziaływań opracowano wskaźnik konkurencyjności: $K = \frac{C \cdot 100\%}{M \cdot P}$ (C = plon badanego gatunku w hodowli mieszanej, M - plon uzyskiwany w monokulturze w danym zagęszczeniu, P - wskaźnik proporcjonalności wysiewu badanego gatunku w hodowli mieszanej). Na podstawie tego wskaźnika stwierdzono, że w warunkach wspólnej hodowli Typha latifolia zyskuje na biomasie w porównaniu z hodowlą w monokulturze, natomiast <u>Phragmites australis</u> traci (rys. 10, 11).

Zmiany w biomasie odbywały się głównie przez zmianę kondycji pędów, a w mniejszym stopniu przez zmianę liczby wytwarzanych pędów.

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Interactions between Phragmites and Typha

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