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Changes in the balance between C_3 and C_4 plants expected in Poland with the global change

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Abstract. We can expect significant changes in the plant cover structure and crop structure due to the climate change, and the response of plants with different photosynthetic pathways to global change may be crucial for agriculture. The paper analyzes the impact of habitat factors connected with the climate change: temperature and concentration of CO_2 in the atmosphere on the change of C_3 and C_4 plants primary production (NPP). The Ehleringer model describing the balance between C_3 and C_4 plants indicates that a shift in the balance in favor of C_4 plants and the increase in CO_2 levels, which has continued since the mid-nineteenth up to the present day, would require a temperature increase by 5–10°C. Nonetheless, this increase is much lower, while the review of previous studies and some phenomena observed in the Poland area: high level of NPP in maize crops and the increased in contribution of C_4 species in the flora indicate the shift in the balance in favor of C_4 plants. This fact can be explained by a factor not included to the Ehleringer model: the availability of water and nitrogen.

Key words: climate change, primary production, photolytic pathways, alien species.

1. Introduction

Climate change, mainly increase of carbon dioxide concentration in the atmosphere and increase of temperature, can lead to changes in the rate of photosynthesis and thus to the changes in primary production (NPP). Examination of reaction of plants with different photosynthetic pathways to global change has great economical importance because we should expect significant changes in the balance between plants with different photosynthetic pathways and, in consequence, in crop structure. Global change can also cause serious disturbances in species structure of phytocoenoses, particularly they can change a balance between of C_3 and C_4 species (Pearcy et al. 1981).

The aim of the paper was to analyze the impact of global change on the intensity of primary production of plants with C_3 and C_4 photosynthesis type. It is possible that complex of interrelated factors (CO_2 level, temperature, water and nitrogen availability) leads to predominance of both C_4 and C_3 plants. This results from the fact that increase of CO_2 level will prefer C_3 photosynthesis (Gifford 1977; Sionit et al. 1981; Rogers et al. 1983; Bhattacharya et al. 1985; Norby et al. 1986; Lindroth et al. 1993; Kimball et al. 2002), but shift of temperature will stimulate C_4 photosynthesis (Kakani & Reddy 2007; Ward et al. 2009). Research conducted in field conditions showed that water or nitrogen deficit can limit positive effects of temperature and CO_2 concentration on primary production (Tissue & Oechel 1987; Diaz et al. 1993; Finzi et al. 2006; Norby et al. 2008), but this effect to concerns mainly production of C_3 plants. The mechanism of this phenomenon will be described in next part of the paper.

According to Esser (1987), the content of CO_2 in the atmosphere increased from 320 to 350 ppm within 30 years (1950–1980). Also Nemani et al. (2003) noted the increase from 337 to 369 ppm in the period from 1980–2000. Wheller et al. (2000) predict that in the end of 21st century the level of CO_2 will reach 700 ppm. Growing level of CO_2

and other greenhouse gases entails the increase in global temperature by 1.5–4.5°C. Since the mid 19th century, the five warmest years have occurred in 1990s and 10 of the 11 warmest years have occurred since 1980 (Pearce 1997). However, we should take into consideration that projected changes demonstrate considerable range of uncertainty (Mitchell et al. 1990). Prediction from 80-ties of previous century assumed that, in 2000 CO_2 level would reach to 650 ppm (Siegenthaler & Oeschger 1987) and those projections proved to be greatly exaggerated. Some observations suggest that the trend of temperature increase terminated at the beginning of 21st century, or temperature increase is interspersed with about 10 years of cooler periods (Easterling & Wehner 2009). Despite all uncertainties, climate change is a real fact and doubts may concern only its scale or reasons.

Kędziora (2008) defined the process of climate changes that occurred in Poland as mediterraeanisation of climate. It is expressed by gradual increase of average air temperature with simultaneous absence of annual precipitation increase and shift of rainfalls to cold months. These changes deteriorate hygrothermic conditions in vegetative season. Similar trend for climate change was observed in the neighboring state of Brandenburg (Holsten et al. 2000).

There is no doubts that climate change is nothing new in the geological history of the Earth and organisms have adapted to the most serious changes over evolutionary timescales. Furthermore, while observing changes in the level of CO_2 in Earth's geological history, we find that low levels of CO_2 correspond with periods of mass extinctions (Ghosh et al. 2005) and enrichment of Earth atmosphere with methane and CO_2 was a possible reason of interrupting of triassic extinction (Ruhl et al. 2011). But the key question today is how will organisms respond to the current, apparently rapid, scale of anthropogenic climate change (Root et al. 2003; Round & Gale 2008).

2. C_3 and C_4 plants, and global change

Studies on effects of CO_2 content and temperature on the primary production size have been carried out since 1960s (Strain & Chase 1966; Ford & Thorne 1967; Rogers et al. 1983; Acock & Allen 1985; Potvin & Strain 1985; Bazzaz 1990; Rozema et al. 1993; Ceulemans et al. 2002). Most models (confirmed by experimental data) assume that NPP will increase as the global change progresses (Nijs & Impens 1993; Jameson et al. 2000; Olesen et al. 2000; Wheeler et al. 2000). The review of the size of primary production for the period from 1982 to 1999 made by Nemani et al. (2003) indicates increasing level of total net primary production (NPP) on a global scale. It has been also confirmed by analysis of changes in NPP of the northern hemisphere grassland ecosystems. This analysis indicated that NPP increased in the second half of 20th century (Bernacki 2012) (Fig. 1). According to common opinion, the cause of NPP rise is increasing content of CO_2 and other greenhouse gases in the atmosphere and consecutive changes induced by it: increase of temperature and lengthening of vegetative season. On the other hand, it is possible that NPP will decline due to the progress of global change as a result of deterioration of humidity conditions in some regions of the globe. Some authors conclude that global change has no influence on the NPP size (Bazzaz 1990; Diaz et al. 1993; Shaw et al. 2002) or its influence is negative, due to water or nitrogen deficit (Diaz et al. 1993; Shaw et al. 2002).

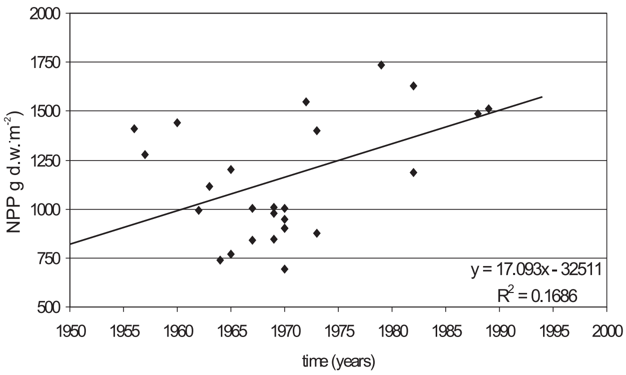


Figure 1. Changes of grasslands NPP in the temperate zone of northern hemisphere (Bernacki 2012)

C_4 metabolism occurs in approximately 1% of plant species. It is about 5% of global biomass and their production is about 30% of global NPP, which means that they have 30% in global carbon fixation (Osborne & Beerling 2006). First C_4 plants appeared around 23–35 million years ago (Oligocene) but they became ecologically important 6–7 million years ago (Miocene) (Ghosh et al. 2005). The C_4 mechanism evolved independently in about 40 groups of plants. This metabolic pathway is especially common for grasses and for sedges. 61% of C_4 plants belong to *Poaceae* (part of them is used in agriculture, e.g. maize, sugar-cane, sorghum, millet and guinea grass) and 18% to *Cyperaceae*. C_4 mechanism is less common for dicotyledons (less than 1% of all dicotyledons).

It should be noted that causes of potential growth of NPP are different for plants with different photosynthetic pathways. For photosynthesis of C_3 plants. increase in concentration of CO_2 in the atmosphere will play important role (Gifford 1977; Sionit et al. 1981; Rogers et al. 1983; Bhattacharya et al. 1985; Norby et al. 1986; Lindroth et al. 1993; Kimball et al. 2002). C_4 plants production is only slightly dependant on CO_2 concentration (Curtis et al. 1989; Poorter 1993), therefore the crucial role will play the increase of temperature (Kakani & Reddy 2007; Ward

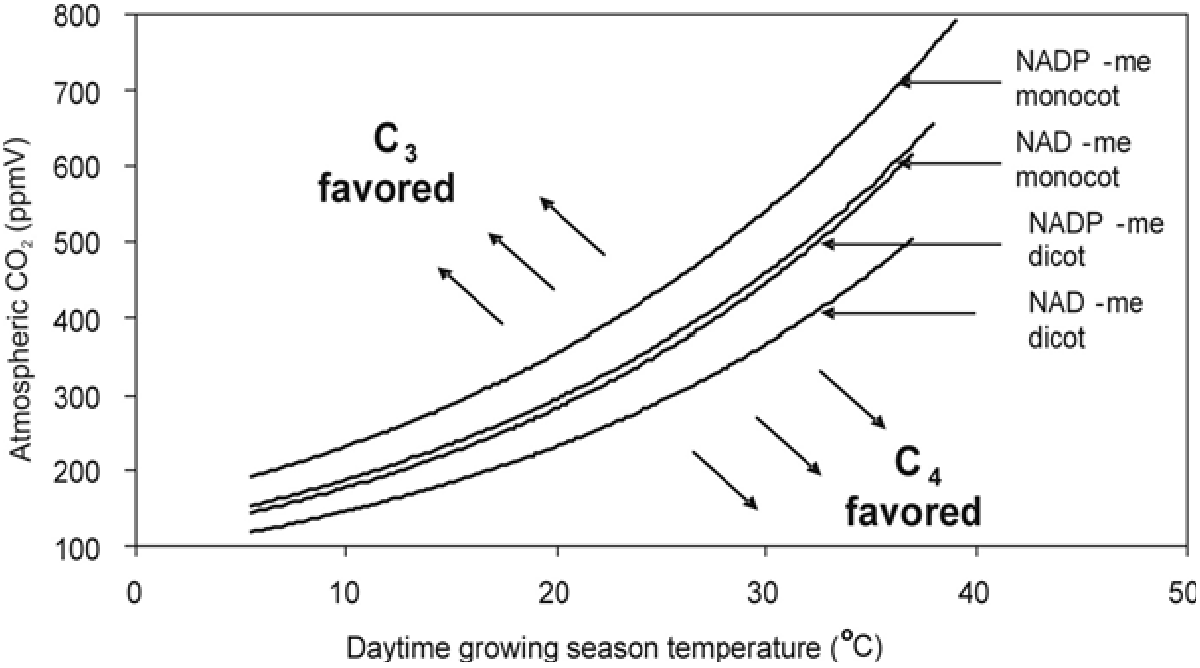


Figure 2. The relationship of balance between C_3 and C_4 plants and CO_2 concentration and temperature (Ehleringer et al. 1997, modified)

et al. 2009). Moreover, the deterioration of hygrotermic conditions and nitrogen deficit limit mainly C_3 plants biomass production. C_4 plants, thanks to double mechanism of carbon dioxide fixation, have lower degree of stomata opening, lower transpiration and thus better water use efficiency (WUE) indicator (Sage & Pearcy 1987; Emmerich 2007). They have also lower requirement for nitrogen as the amount of nitrogen accumulated in both CO_2 acceptors (PEP carboxylase and RuDP carboxylase) is lower than the amount of nitrogen contained in RuDP carboxylase of C_3 plants (Kubien & Sage 2003; Niu et al. 2003). On the other hand, growing CO_2 concentration in the atmosphere can even lead to decline in C_4 plants biomass production (Patterson & Flint 1982).

Ehleringer's model (Ehleringer et al. 1997), published in the ecological literature at the end of the previous century, describes the balance between C_3 and C_4 plants with simultaneous changes of temperature and CO_2 level. According to this model, the balance has the form of exponential curve (Fig. 2). The model also indicates that for the balance to shift in favor of C_4 plants, the increase of CO_2 level that has occurred since mid 19th century to the present would require a temperature increase by 5–10°C. As research shows, this increase is much lower, both globally (Intergovernmental Panel on Climate Change 2007) and locally (Bernacki 2012). At the same time, the review of previous studies indicates balance shifting in favor of C_4 plants (Leakey 2009). This shift can also be confirmed by phenomena observed in the Polish area, such as high level of NPP in the maize crops (Bernacki 2012), or increase in C_4 species in flora.

The increase of temperature and CO_2 level is not a satisfactory explanation for this phenomenon. This fact can be explained by water (and probably nitrogen) availability - factors, not included in Ehleringer's model (Wall et al. 2001; Oliver et al. 2009). The model explaining possible change of balance, caused by global change, should also take into account these factors. Because the system of interrelated factors (CO_2, temperature, water) is very complicated, it is difficult to predict the direction of changes. The balance can move towards dominance of C_3 as well as C_4 plants, depending on the relation between affecting factors.

3. NPP of C_3 and C_4 crops in simulated greenhouse effect and in field conditions: a comparison of trends

Experiment carried out in controlled condition in National Institute of Agro-Environmental Sciences in Tsukuba Japan (Bernacki 1993) showed that the impact of shift of CO_2 concentration on NPP of C_3 (rice) and C_4 (maize) crops was similar, if only temperature increased simultaneously. Doubling of CO_2 concentration with simultaneous 2°C increased of temperature, elevated NPP level of rice 35% and maize NPP 23% but differences between crops was not statistically significant. Successive elevation of CO_2 up to 1200 ppm does not influence neither NPP level nor rice

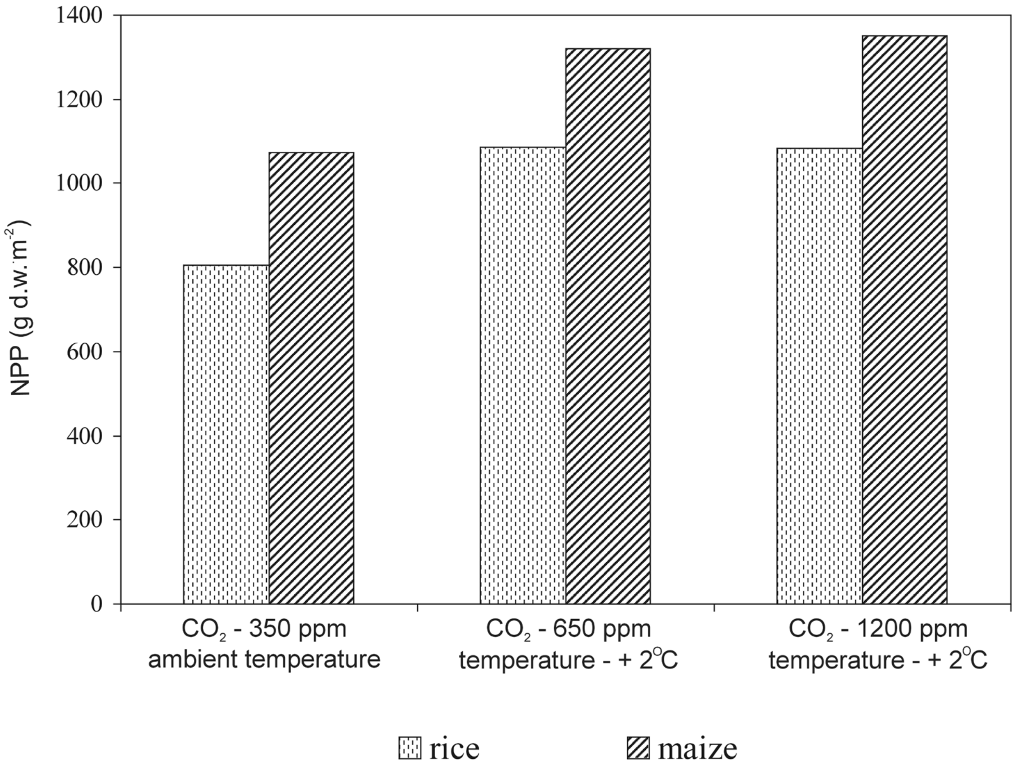
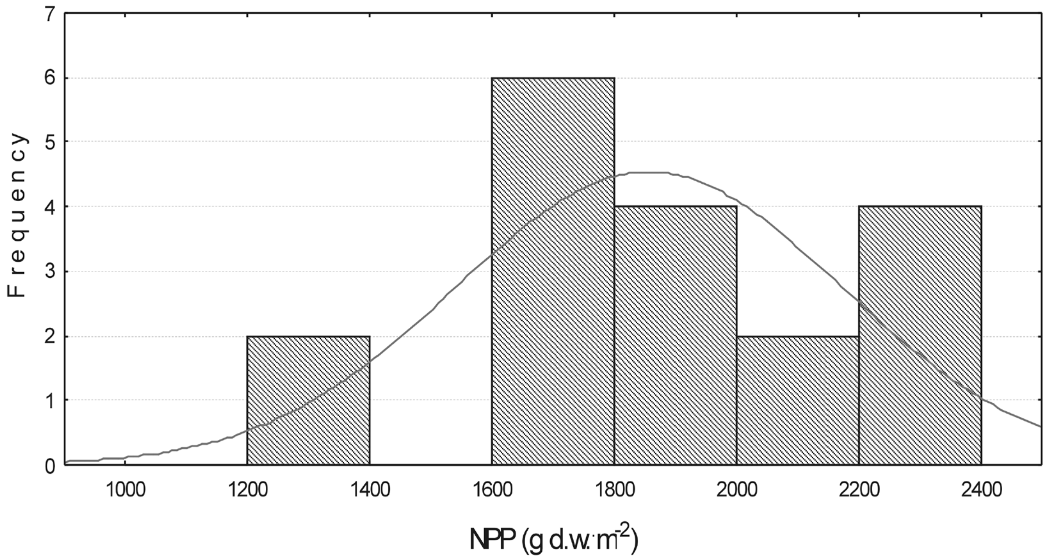
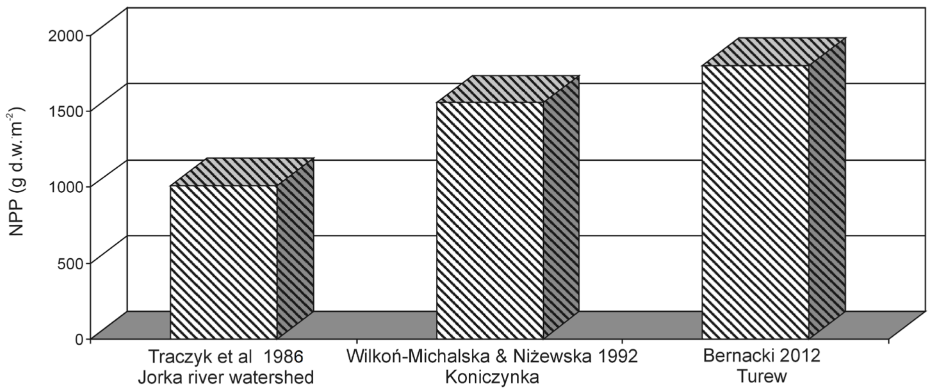


Figure 3. Impact of simulated greenhouse effect on NPP of rice (C_3) and maize (C_4); data from Bernacki (1993)



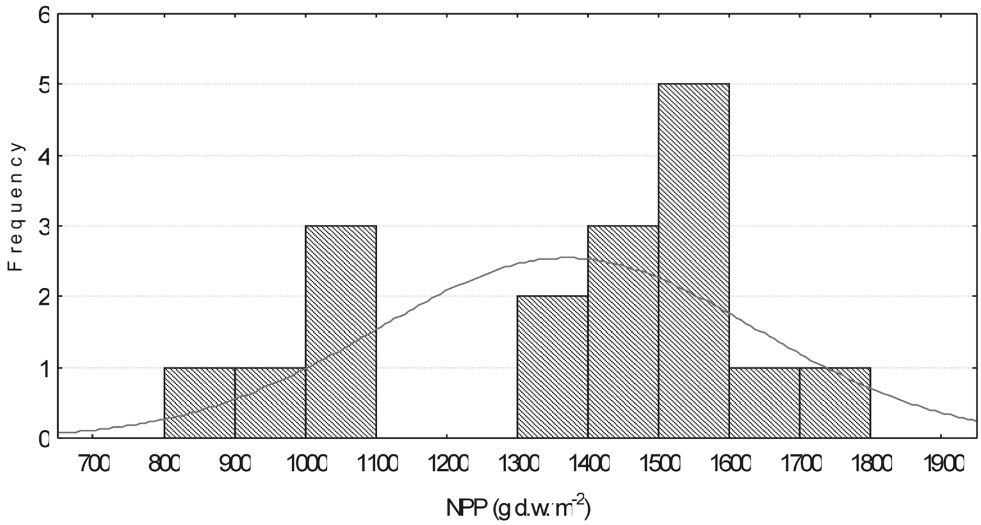
N	mean	range	StD
	g d.w.·m^{-2}		
18	1804.08	1178.67 - 2363.83	329,16

Figure 4. NPP of maize in Turew, West Poland; data from Bernacki (2012)



	Average temperature (°C)	Total of rainfall (mm)
Jorka river watershed (Mazurian Lakeland)	6.8	580
Koniczynka (Chełmińska county)	7.5	554
Turew (Wielkopolska)	8.0	599

Figure 5. Primary production of maize crop in different regions of Poland on the background of climatic conditions (Bernacki, unpublished data)



N	median	ramge	interquartile range
	g s.m. ·m^{-2}		
15	1465.57	868.66 - 1790.45	465.2100

Figure 6. NPP of C_3 plants (winter wheat, rye, triticale oats, potato) in Turew, West Poland; data from: Herbichowa (1969a, b), Kukielska (1973a, b), Pasternak (1974), Bernacki (1992)

and maize (Fig. 3). These results show that the Ehleringer model must be supplemented with additional factors influencing balance between photosynthetic pathways, such as: water regime or nitrogen requirements.

Studies conducted in field conditions in Turew (central Wielkopolska, West Poland) from 1995 to 1997 showed very high primary production of maize fields, exceeding 2300 g d.w. · m^{-2}, with mean other 1800 g d.w. · m^{-2}

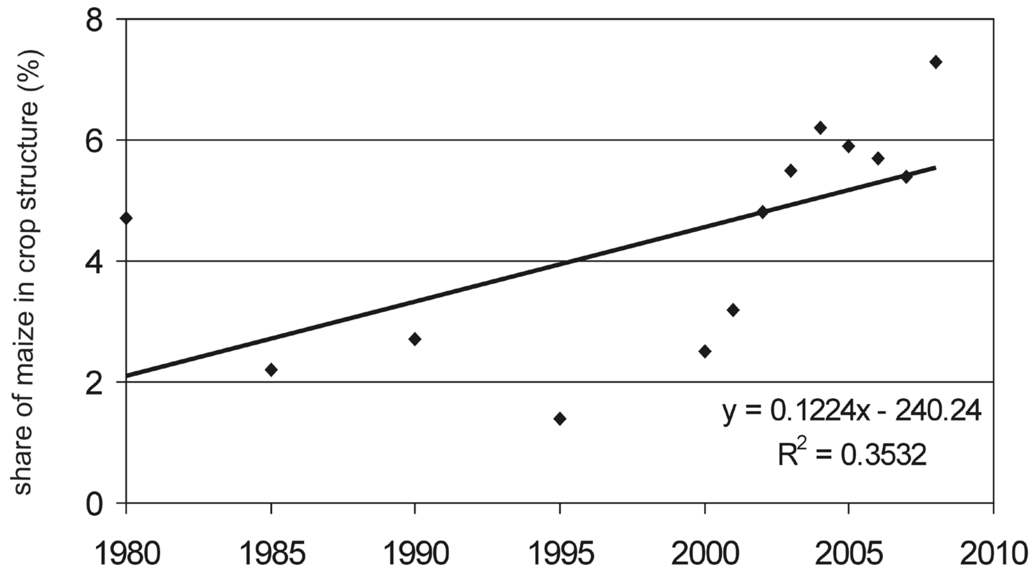


Figure 7. Trend of maize share in the crop's structure in Poland during 30 years (1980 – 2010); the Author's own analysis based on the data of the Central Statistical Office (GUS 2008)

(Fig. 4). Such a high level of NPP was observed in previous studies in Poland only occasionally (Wilkoń Michalska & Niżewska 1992).

Supposition that high level of maize NPP is a result of climate change is supported by comparison of maize NPP in different region of the country, diverse in climate conditions (Fig. 5). Moreover, a comparison of maize NPP in Central Wielkopolska and C_3 crops NPP, documented in the same area in 1966–89, showed considerable differences of ca. 500 g d.w.$\cdot$m^{-2} (Fig. 6). Such results allow to draw conclusion that climate change predicted in Poland (and more broadly for the whole temperate zone) moves balance between photosynthetic pathways towards C_4 photosynthesis. Results presented in this chapter permit the adoption of the thesis that one of the causes of the increase share of maize in the crop structure in Poland observed from the 80s of last century (Fig. 7), may be climate change, preferring C_4 photosynthesis. Therefore, we may expect replacement of wheat with maize in temperate climate zone where changes, such as water deficit, shall prefer C_4 photosynthesis.

4. Changes in flora: invasive and native species with different photosynthetic pathways

Another effect, connected with changes of balance between plants with different photosynthetic pathways in Poland, can be increasing share of alien plants with C_4 mechanism in flora (Table 1). Information about C_4 plants occurrence in Poland have been gathered since 19th century but their share in plant associations is not documented sufficiently. From the middle of 20th century studies covered at least some parts of all regions, and since 1978 data have been collected in ATPOL database (Zając & Zając 2001). Among almost 3000 vascular plants species in Poland (2500 native and 500 alien) about 60 belong to C_4 but in native flora only 5 species represent C_4 photosynthetic pathway. Between 372 species of alien plants in Poland up to 7.5% (28) consist C_4 plants. Between the foreign grass share of C_4 plants is high and reaches 42.9%. Many of C_4 plants are common weeds brought to the area before the industrial era with the crop plants from the Middle East, but their occurrence is not restricted to crop fields, some of them are aggressive invasive plants. Among the most invasive species in Poland, there are no C_4 plants, however, four of them have the status of invasive species (Table 1), and genus: *Setaria, Digitaria, Echinochloa, Eragrostis, Amaranthus,* seem to be potentially invasive.

5. Conclusions

The following conclusions can be drawn from the discussion presented in this paper:

1. Reaction of plants with different photosynthetic pathways to global change is dependent on some interrelated factors and difficult to predict. Uncertainties are

Table 1. Native and alien species with C4 photosynthetic pathway in Poland (invasive species* in bold)

Native species	Alien species
Atriplex glabriuscula Edmondston *Cyperus flavescens* L. *Cyperus fuscus* L. *Eleocharis acicularis* (L.) Roem. & Schult. *Salsola kali* L. subsp. *kali*	*Amaranthus blitoides* S. Watson *Amaranthus chlorostachys* Willd. ***Amaranthus lividus* L.** ***Amaranthus retroflexus* L.** *Atriplex prostrata* Boucher ex DC. *Cenchrus ciliaris* L. *Cynodon dactylon* (L.) Pers. *Digitaria sanguinalis* (L.) Scop. *Dinebra retroflexa* (Vahl) Panz *Echinochloa colonum* (L.) Link ***Echinochloa crus-galli* (L.) P. Beauv.** *Eleusine indica* (L.) Gaertn. *Eragrostis albensis* H. Scholz *Eragrostis amurensis* Prob. *Eragrostis minor* Host *Eragrostis multicaulis* Steud. ***Eragrostis pilosa* (L.) P. Beauv.** *Euphorbia humifusa* Willd. *Euphorbia maculata* L. *Portulaca oleracea* L. *Salsola kali subsp. ruthenica* (Iljin) Soó *Setaria pumila* (Poir.) Roem. & Schult. *Setaria verticillata* (L.) P. Beauv. *Setaria viridis* (L.) P. Beauv. *Sorghum halepense* (L.) Pers. *Tragus racemosus* (L.) All.

*invasive species according to http://www.iop.krakow.pl/ias/Baza.aspx

strengthened by doubts as to the further course of global change. Those include:

- high total primary production of maize (not listed in previous studies),
- the increased share of C_4 species in the Polish flora, including invasive or potentially invasive plants.
- changes in agriculture, especially increasing share of maize in crop structure.

2. The Ehleringer model is not sufficient for explaining reaction of plants with different photosynthetic pathway to global change.

3. Balance of photosynthetic pathways in temperate zone moves towards C_4 domination.

Some results used by author clearly showed increasing role of C_4 plants in Poland.

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