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MISCANTHUS – UNUSUAL GRASS: BIOCHEMICAL AND PHYSIOLOGICAL CHARACTERISTIC: A REVIEW

MISCANTHUS – TRAWA NIEZWYKŁA: CHARAKTERYSTYKA BIOCHEMICZNO-FIZJOLOGICZNA: PRZEGLĄD LITERATUROWY

Abstract: *Miscanthus* × *giganteus* (Giant Miscanthus) is one of the most promising plants cultivated for biomass production. In spite of its origin from south-east Asia and being warm adapted plant it grows well and produces high biomass in temperate latitudes. *Miscanthus* × *giganteus* is a C_4 plant and hence this study presents a brief description of C_4 photosynthesis and the enzymes involved in this process. On the basis of data from current literature, the biochemical bases of relatively high tolerance of miscanthus to cold temperatures (0–15 ^{o}C) were evaluated. Moreover, it was reviewed numerous ecophysiological features of *Miscanthus* × *giganteus* were reviewed (high productivity, low fertiliser and pesticides requirements, possibility to use in phytoremediation) which showed that it is a proecological and environmentally friendly crop. This causes that *Miscanthus* × *giganteus* might be recognize as a leading crop in non-food cultivations.

Keywords: miscanthus, C_4 photosynthesis, chilling tolerance, phytoremediation, allelopathy

Introduction

Plants from genus of *Miscanthus* originate from south-east Asia and are widely distributed in Asia and Pacific Islands. *Miscanthus* belongs to *Poaceae* family and tribe of Andropogoneae [1]. *Miscanthus* is rhizomatous perennial grass reaching height of 5 m and offers very high biomass yield. In 1935 it was introduced into Europe and initially was cultivated in parks and gardens as ornamental plants. Over the past 20 years, there is increasing interest in *Miscanthus* as a raw material for industry (paper production, insulation material) and renewable source of energy. Heating value of *Miscanthus* is about 17–19 MJ $\cdot$ kg^{-1} and is similar to energetic value of wood fuel and it accounts for about 60 % of that of hard coal [2, 3].

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Plants from *Miscanthus* genus are frequently so-called Chinese Grass or Elephant Grass. The most famous representatives of these grasses are: *Miscanthus sinensis, Miscanthus sacchariflorus* and *Miscanthus* × *giganteus* (Giant Miscanthus). *Miscanthus* × *giganteus* is a sterile triploid (2n = 3x = 57) arising through natural crossing of tetraploid *Miscanthus sacchariflorus* (2n = 4x = 76) and diploid (2n = 2x = 38) *Miscanthus sinensis* [4]. Generated hybrid is sterile, does not produce seeds and hence it must be propagated vegetatively by rhizome division or *in vitro* cultures. *Miscanthus* × *giganteus* displays a good balance of traits from each parent, combining rapid growth with a tolerance to low temperatures [5]. *Miscanthus* × *giganteus* (hereafter referred to as miscanthus) is a robust woody perennial which may be cultivated at one site for 15–20 years. It reaches full productivity over the first 3 years after planting. Miscanthus appears in numerous genotypes [3, 6].

Miscanthus is closely related to three important agricultural crops: sugarcane (*Saccharum officinarum*), sorghum (*Sorghum bicolor*) and maize (*Zea mays*). All these crop species are C_4 plants and exhibit high productivity particularly in warmer and well radiated regions.

Miscanthus – C_4 plant (biochemical characteristic)

C_4 plants have evolved mechanisms to improve photosynthetic efficiency and decrease water loss in hot, dry environments. In *Miscanthus*, as in other C_4 plants, CO_2 fixation is a two-step process. CO_2 is initially fixed in the cytosol of mesophyll cells surrounding the bundle sheath [7]. This reaction is catalyzed by *phosphoenolopyruvate carboxylase* (PEPC; EC 4.1.1.31). PEPC is homotetrameric enzyme that has high affinity to CO_2 and is activated by divalent cation [8]. PEPC can fixe CO_2 at very low its concentration and may use CO_2 produced in respiration. PEPC catalyses the β-carboxylation of phosphoenolopyruvate using HCO_3^- as substrate in a reaction that yields oxaloacetate (a four carbon dicarboxylic compound) and phosphate (Pi):

$$\textit{phosphoenolopyruvate}\ \text{(PEP)} + HCO_3^- \rightarrow \text{oxaloacetate (OAA)} + \text{Pi.}$$

Then oxaloacetate is converted to malate by NADPH-malate dehydrogenase:

$$\text{Oxaloacetate} + \text{NADPH} + H^+ \rightarrow \text{malate} + \text{NADP}^+.$$

Formed malate is transported by plazmodesmata to the bundle sheath cells, where it is decarboxylated in reaction catalysed by NADP-malic enzyme (NADP-ME):

$$\text{malate} + \text{NADP}^+ \rightarrow CO_2 + \text{pyruvate} + \text{NADPH} + H^+.$$

Released CO_2 is fixed by Rubisco (*ribulose-1,5-bisphosphate carboxylase/oxygenase*; EC 4.1.1.39) and converted to carbohydrate in the Calvin cycle. Pyruvate (C_3 acid) diffuses back to the mesophyll cells to regenerate phosphoenolopyruvate – primary acceptor of CO_2:

$$\text{pyruvate} + \text{ATP} + \text{Pi} \rightarrow \text{phosphoenolopyruvate} + \text{AMP} + \text{PPi.}$$

This reaction is very important because it leads to regeneration of primary CO_2 acceptor and allows to remaining its concentration at suitable level. Reaction occurs in mesophyll chloroplasts and is catalyzed by *pyruvate orthophosphate dikinase* (PPDK, EC 2.7.9.1). Enzyme action consumes two high-energetic bounds of ATP and requires orthophosphate. PPDK activity is regulated by light. Fully active PPDK is a tetramer that may dissociate at low temperature and it leads to a loss of its activity. Divalent cations (Mn^{2+}, Mg^{2+}, Ca^{2+}), phosphoenolopyruvate, polyols (glycerol, sorbitol) and proline protect PPDK against cold inactivation [9–11].

It is worth to note that among the C_4 plants there are three subtypes characterized according to the type of decarboxylating enzyme in the bundle sheath cells. *Miscanthus* belongs to described above the NADP-malic enzyme (NADP-ME) pathway. Plants using this pathway are characterized by very high *nitrogen use efficiency* (NUE).

The physiological significance of two-step CO_2 fixation process is increasing CO_2 concentration in cells of bundle sheath (it is estimated 10-fold over atmospheric concentration). This leads to elimination of oxygenase activity of Rubisco and carbon loss in photorespiration process. As a result, in favourable environments, C_4 plants are the most productive crops. They show high photosynthetic rates (both interception of solar radiation and CO_2 fixation) and higher water and nitrogen use efficiency. The field trials performed with *Miscanthus* × *giganteus* and *Triticosecale* (C_3 plant) showed that NUE, defined as the ratio of biomass yield to N supply (sum of soil NO_3^- and N fertilization) were 0.35 and 0.14 Mg dry biomass per kg N, respectively for miscanthus and triticale [12].

C_4 plants have high rates of photosynthesis and productivity but this is realized in favourable conditions – high radiation and warm, humid environments. In temperate zones, low temperature is a major constraint limiting rate of photosynthesis and consequently productivity of C_4 plants. *Miscanthus* × *giganteus* appears to be unusual among C_4 species and cultivated at 52° northern latitude produces 30 tonnes of dry matter per hectare per year, exceeding the most productive C_3 crops [13].

Cold tolerance of *Miscanthus* × *giganteus*

Low temperature is a major factor that influences plant metabolism and physiology and affects its productivity. The most of C_4 species influenced by chilling temperatures (0–15 °C) react by apparent reduction of CO_2 assimilation and consequently, utilization of absorbed solar energy is limited. This leads to photoinhibition and photodamage of photosynthetic apparatus. *Miscanthus* × *giganteus* is relatively tolerant to chilling temperatures (avoids these damages) and similarly to maize may be cultivated in temperate climates. Nevertheless, in comparison with maize, miscanthus considerably better tolerates suboptimal conditions, particularly too low temperatures in spring and autumn [14]. Maize growing at 14 °C shows 90 % reduction in CO_2 uptake comparing with plants grown at 25 °C, whereas in *Miscanthus* × *giganteus* this negative response does not happen [15, 16]. Some researchers have postulated that Rubisco is the most likely candidate for limiting C_4 photosynthesis at chilling temperatures [17]. However experiments conducted by Wang et al [18] on Rubisco from *Miscanthus* × *giganteus* grown at 14 and 25 ^oC and *Zea mays* grown at 25 ^oC showed that there were no significant differences in enzyme catalytic proprieties. Rubisco did not differ significantly, either between the two species or between growth temperature. These results suggest that higher cold tolerance of miscanthus than maize does not result from Rubisco activity [18]. Wang et al [11] concluded that pyruvate orthophosphate dikinase (PPDK) is responsible for greater photosynthetic capacity in miscanthus than other C_4 species cultivated under suboptimal temperature. In experiments of Wang et al [11], lowering of growth temperature from 25 to 14 ^oC caused different reaction in miscanthus and maize. On the first day at low temperature, PPDK protein declined slightly in miscanthus but then accumulated above the initial level and was nearly doubled after 7 days, whereas Rubisco level did not change significantly. In contrast to miscanthus, PPDK in maize leaves declined throughout in chilling period and Rubisco level was also significantly reduced. Naidu et al [19] obtained similar results. In miscanthus low temperature caused accumulation of PPDK protein while level of Rubisco remained unaffected. Whereas in maize leaves there was recorded decrease in quantity and activity of both crucial enzymes – PPDK and Rubisco.

Concluding, it can be stated that increases in either protein content and PPDK activity in leaves of C_4 plants growing in chilling conditions may be one of the mechanisms increasing their tolerance to low temperatures.

As mentioned above, low temperatures can disrupt balance between absorbed excitation energy of light and its utilization by photosynthetic apparatus [20]. Low temperatures decrease rates of CO_2 uptake and assimilation, and in turn, plant demand for ATP and NADPH is markedly reduced. Consequently, it leads to secondary effects associated with formation and accumulation of *reactive oxygen species* (ROS). The most important ROS are: superoxide ($O_2^{\bullet -}$), hydroxyl radical ($OH^\bullet$), hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$). These molecules are potentially harmful and may attack cellular components (macromolecules and membranes) and cause serious damage of photosynthetic apparatus (photoinhibition), ultimately leading to severe cellular damage. Plants have the capacity to eliminate ROS and antioxidant molecules such as ascorbic acid, carotenoids, glutathione play important role in this protective system. Carotenoids, lipid-soluble pigments presented in chloroplasts, have the ability to dissipation of surplus excitation energy and act as quencher of its excess and hence they are the main compounds involved in preventing photoinhibition. A particular class of carotenoids – the xananthopylls – play a key role in protection against oxidative damage. Zeaxanthin, the de-epoxidised form, better dissipates excitation energy and is derived from the epoxidised pigments violaxantin. The rapid changes between the two forms, brought about by special enzymes, constitute the "xantophyll cycle". It is worth to note that in chilling conditions miscanthus avoids photooxidative damages by maintaining a high rate of CO_2 uptake and assimilation, and in turn increased utilization of absorbed light energy [13]. On the other hand, in this plant very efficiently operates described above mechanism of non-photochemical quenching of excitation energy. This correlates with large increase in xanthophylls content and its de-epoxidation [16]. In comparison with the other C_4 plants, *Miscanthus × giganteus* has a lower temperature optimum for light-saturated photosynthesis [15].

It is worth noting that *Miscanthus* × *giganteus* shows high cold susceptibility, especially to freezing temperature, in the first year after planting. Periods of frost, typical during early spring and winter, may result in poor plants' survival and are potential obstacles to the establishment of miscanthus in northern regions of Europe [21–23]. Plazek et al [24] suggested that frost susceptibility of miscanthus is mainly caused by sensitivity of shoot apical meristems to frost. Farrell at al [23] have investigated genotypic variation in the *base temperature* (T_b) for shoot emergence and in the lethal temperature for shoots in four *Miscanthus* genotypes. In all genotypes, lowering temperature increased the time of shoot emergence. T_b for *Miscanthus* × *giganteus* accounted 8.5 °C and was slight higher compared with *Miscanthus sinensis*. All examined genotypes exhibited considerable leaf damage following exposure to –8 °C and they might be classed as freezing sensitive [23]. However, taking into account the information that tropical grasses fall within the temperature range –1.8 °C to –4.3 °C [25], it might be concluded that plants from *Miscanthus* genus are relatively tolerant to non severe frost. In the case of *Miscanthus* × *giganteus*, the lethal temperature at which 50 % of the shoots were killed was estimated as –8 °C [23].

Other promising features of *Miscanthus* × *giganteus*

Miscanthus × *giganteus* has several positive ecophysiological traits causing that is considered as environmentally benignant plant:

– **High productivity.** At temperate climate conditions miscanthus yield reaches 20–30 tonnes dry matter per hectar per year (since the second or third year after planting when the crop is well established) and it may be higher – 40 tonnes dry matter $year^{-1}$ ha^{-1} – in southern Europe (Mediterranean regions) with irrigation [12, 26, 27].

The first side-by-side large-scale field trials conducted on *Zea mays* and *Miscanthus* × *giganteus* in the U.S. Corn Belt (Illinois) showed that miscanthus was 59 % more productive than modern lines of grain maize bred for high productivity [28]. Nevertheless, it is interesting that examinations concerning some important parameters of photosynthesis (rate of both phosphoenolopyruvate carboxylation and phosphoenolopyruvate regeneration, quantum efficiency of CO_2 assimilation) demonstrated that they were higher in maize than in miscanthus. However, these biochemical and photochemical traits of maize were not enough to match up to miscanthus in productivity. Dohleman and Long [28] state that higher productivity of miscanthus in comparison with maize is related to larger leaf area and its longer growing season. Consequently, miscanthus intercepts more PAR (*photosynthetically active radiation*) and longer continues photosynthesis. Length of growing season (average for two years) for maize was 125 days whereas for miscanthus it was 199 days (60 % longer than for maize).

Dohleman et al [29] conducted field trials to find the reasons for hugely higher biomass production of *Miscanthus* × *giganteus* in comparison with *Panicum virgatum* (switchgrass; such as miscanthus is C_4 perennial grass considered as bioenergy crop). They concluded that there are numerous factors determined greater productivity of miscanthus: almost 40 % higher photosynthetic rates, significantly higher both nitrogen and water use efficiencies, lower respiration, larger leaf canopy and its more vertical standing (more radiation penetrates into the deeper canopy).

– **Low fertiliser requirements.** The most field trials conducted at different sites showed that mineral fertilisation (particularly nitrogen supply) does not improve significantly yield of miscanthus especially in the case of full established plantations [26, 30–34]. In initial seasons of planting fertilisation may lead to an increase in above-ground biomass accumulation [35, 36]. Field experiments in southern regions of Europe demonstrated that nitrogen fertilisation significantly increase dry mass of aboveground biomass when water was not limiting (trials with irrigation) [36, 37].

Experiments conducted by Kalembasa et al [35] on five clones of *Miscanthus*, after two years of cultivation, showed that $N_{60}P_{50}K_{100}$ fertilisation cause decrease in dry mass of underground parts (rhizomes + roots). Amougou et al [33] stated that underground biomass was not significantly affected by nitrogen fertilization (120 kg N ha^{-1} $year^{-1}$) but it tended to decrease under N fertilization, particularly on 2-year-old miscanthus stand.

It is noteworthy that long-term trials (14 years) conducted in different locations in Europe also demonstrate that nitrogen fertilisation does not improve growth and biomass productivity of *Miscanthus* × *giganteus* [32]. This unpredictable response of miscanthus to nitrogen application results from very efficient minerals' movement within the plant during the growing season. Rhizomes act as a storage organ and in autumn nitrogen and other nutrients are translocated from aboveground parts (stem + leaves) to rhizome. In subsequent spring season, nutrients stored in rhizome are remobilized and transported into new growing shoots. This causes that miscanthus is partly independent of the actual nutrient supply from soil [26, 38]. Kalembasa et al [39] investigated 5 clones of *Miscanthus* in second year of cultivation, at five different term of growing season (from June to October) and they demonstrated that total nitrogen content was the highest in June and lowered significantly in subsequent months. At the end of growing season (in October) N concentration in dry matter lowered by 5.5-fold on average for all clones comparing with its concentration in June.

Effective minerals' translocation is very profitable phenomenon also in aspect of biomass utilization and its combustion quality. Low concentration of nutrients in harvestable biomass results in reduction of undesirable compounds released during combustion such as SO_2, NO_x, HCl, dioxin. Delayed harvest date (over winter) reduces moisture, ash and nutrient contents in yield and hence is an effective method to improve the biomass quality for combustion [2, 22, 40].

– **Poor needs for crop protection.** In well established plantations (from year two or three onwards), miscanthus very effectively competes with weeds. Mechanical or chemical weed control is necessary during crop establishment [26, 32, 34]. In subsequent years, fast growing plants and leaf litter layer on the soil create conditions that significantly limit growth of other plants and hence application of herbicides is not necessary every year. It is likely that *Miscanthus* × *giganteus* such as other representatives of *Poaceae* family shows high allelopathic activity [41]. It was documented that *Miscanthus transmorrisonensis* and *Miscanthus floridulus* (species growing in Taiwan) produce phenolic compounds that inhibit growth of other plants [1, 41, 42]. Miscanthus is characterized by relatively high resistence to pests and diseases and chemical products against them are not necessary [26, 32, 34].

– **Potential possibility to using in phytoremediation.** *Miscanthus* ssp. may grow on acidic soils where increases bioavailability of heavy metals and in turn raises their phytotoxicity [43, 44]. Under low pH conditions aluminium (Al), the third most abundant element in earth's crust, is a major soil mineral constituent that may restrict plant growth. It has been reported that Al promotes growth of *Miscanthus sinesis* and is considered as beneficial element for this plant [45]. Besides, it was shown that *Miscanthus sinesis* is also tolerant to other heavy metals: chromiun and zinc [44]. Aluminium presented in plant tissues may enhance herbivore defence and promote phosphorus uptake [45]. Arduini et al [46] have shown that *Miscanthus* × *giganteus* is not particularly tolerant to cadmium. Their experiments conducted in a controlled environment demonstrated that biomass production is declined by 50 % with cadmium concentrations ranging from 0.75 to 2.25 mg · dm^{-3} in nutrient solution and Cd concentration in roots was more than 10-fold higher than that of the shoot. However, these authors suggest that even Cd-sensitive species like miscanthus could effectively accumulate cadmium and widen the range of species using in phytoremediation.

Plantations of *Miscanthus* ssp. may prevent and reduce soil erosion as well as stabilize and extract contaminations from soil [47, 48].

Conclusions

Miscanthus × *giganteus* in spite being C_4 plant adapted to warmer climate, is relatively tolerant to chilling temperatures and in temperate zones its growth is fast and biomass production very high. *Miscanthus* × *giganteus* displays a good combination between high productivity and efficiencies in using of water, nitrogen and solar radiation. Besides, it shows numerous ecophysiological traits causing that it might be recognize as leading crop in non-food cultivations.

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MISCANTHUS – TRAWA NIEZWYKŁA: CHARAKTERYSTYKA BIOCHEMICZNO-FIZJOLOGICZNA: PRZEGLĄD LITERATUROWY

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Abstrakt: *Miscanthus × giganteus* (Miskant olbrzymi) jest jedną z bardziej obiecujących tzw. roślin alternatywnych uprawianych z przeznaczeniem na cele energetyczne. Pomimo że pochodzi z południowo-

-wschodniej Azji i jest rośliną ciepłolubną, to bardzo dobrze rośnie i charakteryzuje się wysoką produktywnością w strefie umiarkowanych szerokości geograficznych. *Miscanthus × giganteus* jest rośliną typu C_4, dlatego w pracy przedstawiono krótki opis procesu fotosyntetycznego wiązania CO_2 w tzw. szlaku C_4 oraz uczestniczących w nim enzymów. Korzystając z najnowszych danych literaturowych, przeanalizowano podstawy biochemiczne stosunkowo dużej odporności tej rośliny na niskie temperatury (0–15 ^{o}C). Opisano również szereg ekofizjologicznych właściwości *Miscanthus × giganteus* (wysoka produktywność, niewielkie wymagania nawozowe, brak konieczności stosowania pestycydów, możliwość wykorzystania w procesach fitoremediacji), które sprawiają, że jest on określany jako roślina ekologiczna i szczególnie przyjazna środowisku. Opisane cechy rośliny sprawiają, że można ją uznać za lidera wśród roślin uprawianych na cele nieżywnościowe.

Słowa kluczowe: miskantus, tolerancja na chłód, C_4 fotosynteza, fitoremediacja, allelopatia