Predicting Biomass Production from Plant Robustness and Germination Efficiency by Calorespirometry

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Abstract

Respiration traits allow calculating temperature-dependent carbon use efficiency and can serve as biomarkers for the prediction of growth and biomass formation. While photosynthesis is responsible for capturing CO_2, respiration critically manages the destiny of structurally integrated CO_2 by regulating the use of energy and substances. The efficient interplay of cytochrome and alternative respiration pathways determines plant performance upon permanently changing and interacting abiotic and biotic environment. Thus, respiration traits are central for high biomass production and yield stability based on multi-stress tolerance. Hence, calorespirometry is a useful functional tool for pre-breeding that can

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Dedicated to Lee Hansen in honor of his great contribution to science by driving technology development and supporting its application.

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discriminate plants based on genetic differences in respiration traits. Although it was earlier suggested that the methodology could be valuable in breeding programs to improve temperature-dependent growth performance, this concept had never been applied in global breeding on biomass production. This predictive tool can be applied as an efficient mean (1) to identify differences in germination efficiency among genotypes or through management practice in seed technology, (2) to select plants in conventional breeding, and (3) to identify relevant genomics-based functional markers for temperature-dependent multi-stress tolerance and yield stability. From respiration-related genes, alternative oxidase is a promising candidate for functional marker development. It relates to both germination efficiency and plant robustness linked to biomass yield stability.

Keywords

Calorespirometry • Alternative respiration • Germination efficiency • Genomics • Functional marker development

5.1 Introduction

Breeding on high-level and stable plant biomass production is important, when (a) biomass is directly used as harvest material for specific purposes, such as for fuels (see other chapters in this book), or (b) when biomass can serve as an indirect trait that is associated to final crop production, such as grain yield. The level of biomass production can strongly vary depending on environmental circumstances, which is threatening yield stability. Temperature is a major factor in this scenario. Thus, climate change as well as regional-specific temperature distribution are important issues. However, temperature needs to be seen in the context. It interacts permanently with the complex and variable diversity of abiotic and biotic factors with chaotic effects on plant growth performance. Depending on the region, individual factors, such as water and nutrient availability, can play a minor or major role and also vary in intensity during the plants life cycle. Plant genotypes that are more robust, which means they can tolerate a wider range of diverse and complex environmental conditions, will be more stable in growth performance. Therefore, it is important to recognize robustness as a novel breeding trait linked to yield stability (Arnholdt-Schmitt et al. 2006; Cardoso and Arnholdt-Schmitt 2013). Robustness is based on the capacity to respond upon environmental changes by highly adaptive, molecular-physiological plasticity.

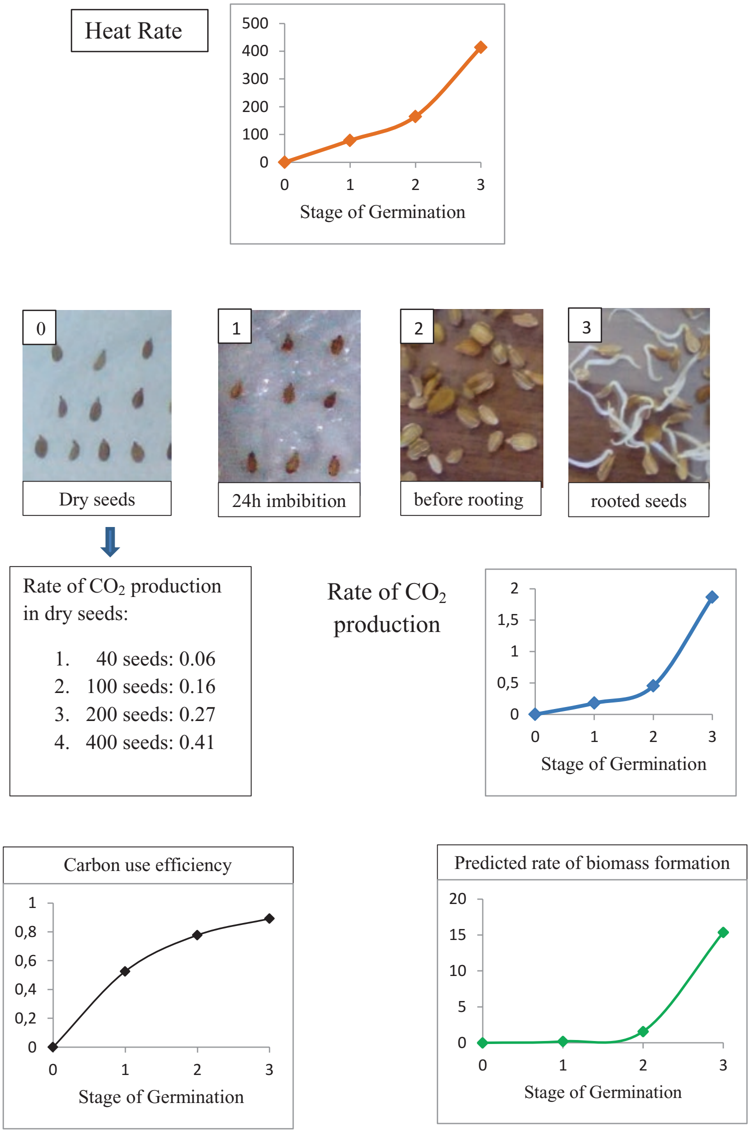
In order to know whether a plant genotype is robust and shows 'stability in biomass production', testing of many different environments is required (e.g., Mühleisen et al. 2014). The term 'environmental condition' must consider also the availability and effectiveness of native endophytes, such as AMFs, *Rhizobia*, bacteria, and others. Also management practices need to be considered, such as pretreatment of seeds, soil management, irrigation, fertilizing, endophyte inoculation, and pesticide or other chemical inputs. Therefore, testing of environmental conditions is highly time-consuming, costly, and labor-intensive. So far, no reliable method exists that can reproducibly predict complex multi-stress tolerance that leads to robustness of plants in a satisfying way. Recently developed methods for high-throughput phenotyping platforms tend to be of high cost and therefore turn themselves to be questionable in view of practical significance for private breeders and agriculture. Translation of extremely expensive genomics data to plant improvement strategies remains a challenge with no clear perspective for efficient and low-cost options. Thus, tool development with high predictive power is supposed to lead to breakthrough advancement for the economic efficiency of prebreeding efforts.

5.1.1 Calorespirometry for Prediction of Germination Efficiency and Seedling Vigor

Germination efficiency varies between plant species. It is supposed that evolutionary fitness is closely linked to germination efficiency (Parsons 2012). Also, it is widely known that germination efficiency in agriculture and horticulture practice can have relevant effects on final yields (e.g., Tian et al. 2014). Related to forestry, it was shown in *Pinus ponderosa* that metabolic heat rate measurements were the most important seedling characteristic that allowed predicting mature-tree performance. Increased metabolic heat rate in seedlings corresponded with greater vigor of mature trees (Momen et al. 2004). However, so far, it is not common to explore improvement in germination efficiency through breeding.

Germination efficiency concerns both (a) induction of germination linked to speed and (b) seedling growth and development. Recently, molecular research efforts are increased to identify genetic components linked to germination (e.g., Wang et al. 2016; Yuan et al. 2016a, b). In agricultural research, special focus is dedicated to improve germination efficiency through management practices via diverse physical pretreatment strategies that aim to substitute chemicals (reviewed in Paparella et al. 2015; De Sousa et al. 2016). Magnetic seed treatment, which provokes changes in energy status of seed cells and molecules, seems to be especially promising as a general strategy across species (e.g., De Souza et al. 2006, 2014; Matwijczuk et al. 2011; Paparella et al. 2015).

Water control and a temperature-dependent change in energy metabolism are of key importance for inducing germination. Germination speed depends on the species. In carrot, germination is slow. Thus, competition through rapidly growing weed can have serious effects on yield-determining carrot growth performance. After imbibition, mitochondria and thus respiration are immediately activated (Paszkiewicz et al. 2017). Therefore, it is reasonable to assume that calorespirometry provides an efficient tool for monitoring and predicting the germination process. Calorespirometry can measure temperature-dependent heat rate changes and CO_2 production (Hansen et al. 2005). Figure 5.1 demonstrates application of the methodology and shows calorespirometry data for carrot seed germination measured at 25 °C. From measured values of heat rate and the rate of CO_2 production, the oxycaloric equivalent and carbon use efficiency can be calculated, and the rate of



Method for calculating carbon use efficiency and rate of biomass formation described in Hansen et al. 2005; Arnholdt-Schmitt 2017

Fig. 5.1 Measuring metabolic heat rate (in μJ s^{-1}) and CO_2 production rate (in $mmols^{-1}$) of germinating carrot seeds by calorespirometry biomass formation can be predicted (see detailed step-by-step protocol in Arnholdt-Schmitt 2017). Consequently, when performed under standardized conditions, calorespirometry can be used for both (1) developing biomarker for genetic discrimination and (2) evaluating seed technology strategies.

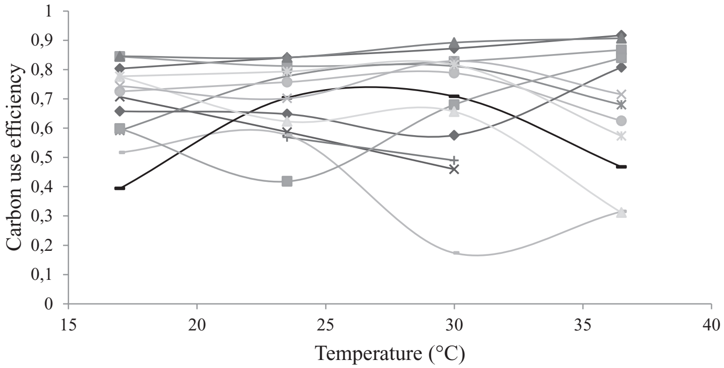
5.1.2 Calorespirometry for Genotype Selection on Stable Biomass Production

Calorespirometry was developed as a tool to understand how plant metabolism acclimates and responds to changes in environment by adapted growth performance (Hansen et al. 1997, 2005). A literature review showed the dominant role of temperature on carbon use efficiency when measured in growing plant material (Hansen et al. 2009). The congruency between temperature-dependent plant growth performance curves and the temperature distribution curve specific for a region can strongly influence the fitness of plants in view of biomass production in that region (Arnholdt-Schmitt et al. 2016). Thus, regional-specific selection of cultivars with defined temperature-dependent growth performance curves and climate change will affect regional biomass production. It was earlier suggested that calorespirometry could be helpful in selecting plants for temperature-dependent growth performance (Hansen et al. 1997; Taylor et al. 1998). No other method can do these measurements and prediction in a rapid way. However, the basic concept was never translated and applied into a breeding tool for major crops.

Biomass production is species-dependent. It relies on the response of target meristems for biomass production to developmental and environmental signaling. The development of calorespirometry as a pre-breeding tool was firstly promoted for carrot (Nogales et al. 2013, 2014). By using a small number of inbred lines, calorespirometry could be shown to identify genotype-specific optimum temperatures and low-temperature limits for tap root biomass growth. The approach was now advanced to diverse crop species, and the method is currently under final validation in the lab of the corresponding author. The '***T***emperature-dependent ***G***rowth ***E***fficiency pattern index' (TGE pattern index) is here introduced as a novel trait for the characterization of genotypes. Figure 5.2a, b gives examples, where calorespirometry was applied to spring wheat cultivars. Figure 5.2a demonstrates the potential of the methodology to indicate genotypes with higher yield stability. TGE pattern indices are compared between genotypes with differences in yield stability (Fig. 5.2a A, B). In Fig. 5.2b, it can be seen that calorespirometry data can help to identify strategies for within-cultivar improvement through selecting at both temperature extremes of the genotype-specific optimal growing temperatures. This confirms results obtained already for carrot tap root biomass yields (Nogales et al. 2014). Figure 5.3 shows that winter cereals (here winter barley) can be easily discriminated from spring cereals already at seedling stage by rapid TGE pattern indexing at higher temperatures (Fig. 5.2). It also seems to justify the stable standing of reference barley cultivars in the market through a higher and more stable temperature-dependent growth efficiency pattern in comparison to breeding lines.

a

A. TGE-Pattern-Index pointing to genetic variation among cultivars with known diversity in yield stability



B. TGE-Pattern-Indices of three cultivars with high yield stability in the field

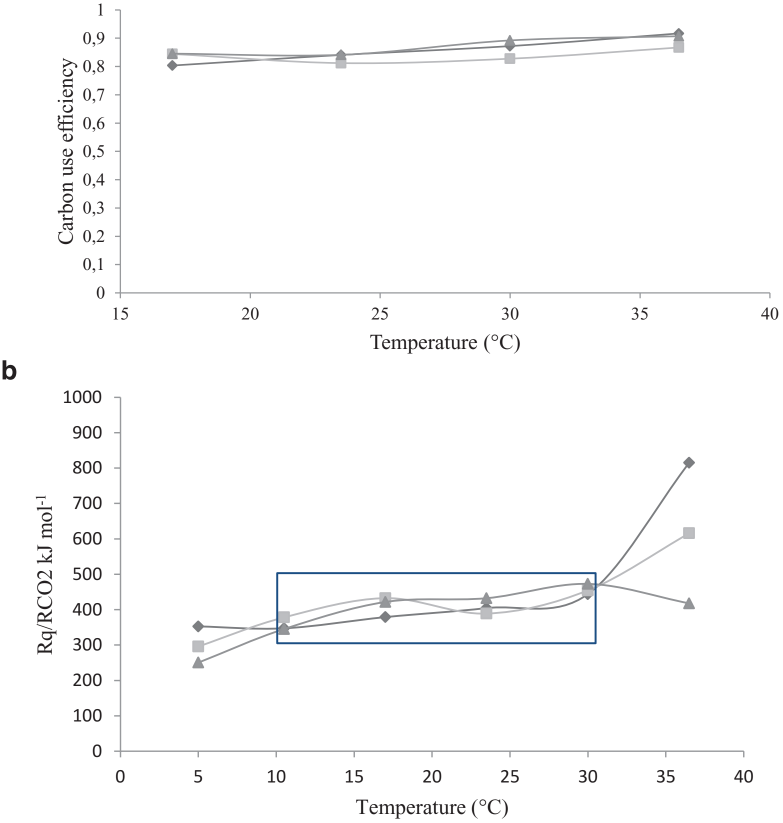
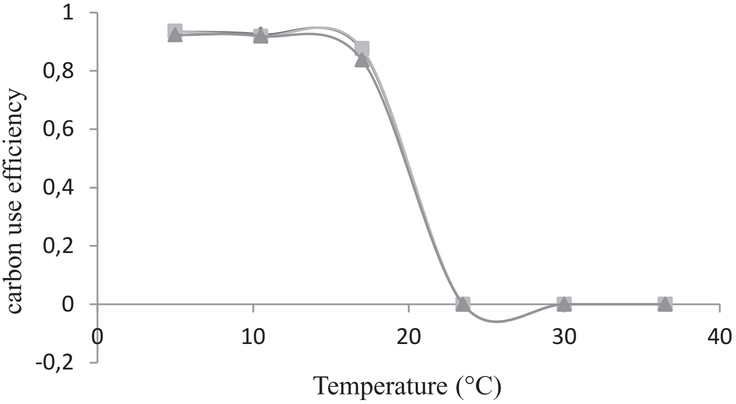


Fig. 5.2 (**a**) 'Temperature-dependent growth efficiency pattern indices' of spring wheat cultivars (TGE pattern indices). Unpublished preliminary results (Arnholdt-Schmitt) shown here to highlight the capacity of calorespirometry for predicting yield performance of cereal genotypes. (A) A TGE pattern index pointing to genetic variation among cultivars with known diversity in yield stability. (B) TGE pattern indices of three cultivars with high-yield stability in the field. (**b**) Temperature-dependent genetic variation identified within a spring wheat cultivar by the help of calorespirometry. The three curves present each a bulked sample of six seedlings (Arnholdt-Schmitt, unpublished)

A. TGE-Pattern-Index for three reference cultivars



B. TGE-Pattern-Index for breeding lines in comparison to the three reference cultivars

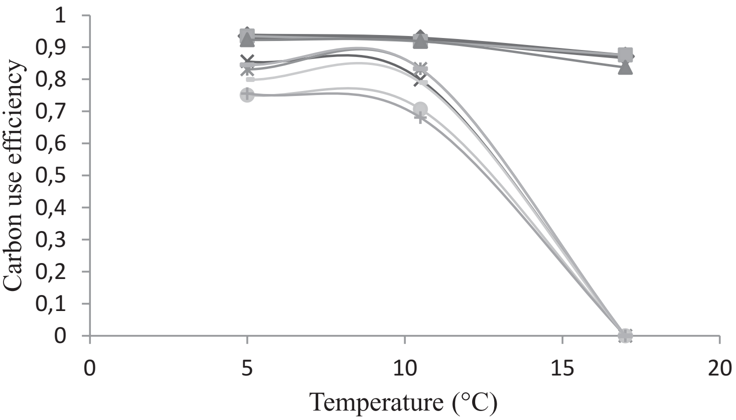


Fig. 5.3 TGE pattern indices of three reference cultivars (**a** and **b**: *upper curves*) and breeding material from winter barley (**b**: *lower curves*); unpublished preliminary results (Arnholdt-Schmitt) shown here to highlight the capacity of calorespirometry as a pre-breeding tool in cereal breeding; TGE pattern indexing discriminates genotypes by (1) level and (2) pattern of temperature-dependent carbon use efficiency. (**a**) TGE pattern index for three reference cultivars. (**b**) TGE pattern index for breeding lines in comparison to the three reference cultivars

5.1.3 Calorespirometry: A Tool for Evaluating the Relevance of Genomics-Based Data

As shown before, calorespirometry is appropriate to select plants in conventional breeding. Thus, the method allows selecting plants of any genetic background for effects on growth performance and yield stability. Consequently, it can be used as functional tool for validating all kinds of genomics-based candidate markers for their effect on biomass production. In the same way, calorespirometry could be applied for functional analysis of holobionts to confirm the effect of plant-microbiome interaction (Arnholdt-Schmitt et al. 2014; Nogales et al. 2016).

Most critical for applying calorespirometry is deep knowledge in physiology. This is important to establish a species-dependent, sophisticated strategy for choosing the correct target meristems and developmental stages for measuring. Data need to be retrieved from the same tissue simultaneously for genomics and for calorespirometry. For example, in order to link genomics data and predictive calorespirometry for carrot root biomass production, analyses need to be performed in the central tap root meristem, the root cambium, where 'the decisions' for secondary root growth are taken through cell identity and complex metabolic regulation in interaction with environment (Arnholdt-Schmitt 1995, 1999, 2004, 2005a, b; Arnholdt-Schmitt et al. 2006; Nogales et al. 2013, 2014). On the other hand, for predicting biomass production in cereals, calorespirometry needs to be performed in germinating seeds, when the focus is on germination efficiency or in growing tissue of seedlings in order to predict yield stability by the TGE pattern index.

Photosynthesis is the main focus when aiming to improve biomass production by breeding. However, it is becoming increasingly evident that mitochondria are the first to respond upon environmental signaling. Respiration with a special relevance of alternative oxidase seems to be critically involved in regulating the efficiency also of photosynthesis (Dinakar et al. 2016).

Respiration traits and, especially, the alternative oxidase (AOX) have been proposed as marker sources for molecular breeding on plant robustness (Arnholdt-Schmitt et al. 2006; Cardoso and Arnholdt-Schmitt 2013: Arnholdt-Schmitt 2017). It is increasingly accepted that adaptive respiration and the genes involved in normal and alternative respiration pathways have bottleneck function for molecular and metabolic cell reprogramming under abiotic and biotic stressful conditions (reviewed in Vanlerberghe 2013; Arnholdt-Schmitt et al. 2015). AOX is the key enzyme of alternative respiration. It consists of a small family of genes that belong either to subfamily *AOX1* or *AOX2* (Costa et al. 2014, 2017). Recently, it could be shown in primary carrot cultures that stress-induced accumulation of *DcAOX1* and *DcAOX2a* transcripts during the lag phase of adaptive cell reprogramming coincided with a critical time point for structural biomass prediction performed by calorespirometry (Campos et al. 2016).

Cytochrome c oxidase (COX) and AOX use natural oxygen isotopes O^{16} and O^{18} to a different extent (Guy et al. 1989; Ribas-Carbo et al. 2005). This allows calculating from oxygen consumption and isotope analysis the extent of normal and alternative respiration. Combining calorespirometry in a tool kit with oxygen consumption measurements and oxygen isotope discrimination will enable to identify candidate genes from respiration for a given meristem or growing plant material that determine biomass growth (Arnholdt-Schmitt et al. 2016). Once the higher relevance of one or the other respiration pathways or of both is confirmed, functional markers can be identified in the candidate gene. Alternatively, gene editing could be applied to introduce target polymorphisms. In any case, selected plants that contain defined functional markers or marker patterns could then be evaluated by TGE pattern indexing as described before.

There are some indications in literature that *AOX* genes might also play a relevant role for regulating germination efficiency. Yentur and Leopold (1976) observed a transition from predominantly alternative respiration at the initial phase of germination to normal respiration after imbibition between 4 and 8 h in soybean. Alternative respiration was linked to germination itself but also to the rate of seedling growth and chlorophyll synthesis. Similar results were reported for other species also (Yentur and Leopold 1976; Esashi et al. 1981). Germination in its early stages was also shown to be sensitive to lower O_2 tension. This supports the relevance of alternative respiration at that time, since AOX has a lower affinity to O_2 than COX (Bonner 1973; cited in Yentur and Leopold 1976). In dry and mature seeds of *Arabidopsis thaliana* as well as during early germination, Saisho et al. (2001) and Clifton et al. (2006) found high expression of *AOX2*. The level of *AOX2* transcript accumulation decreased rapidly during germination (after 12 h) and remained low thereafter. Also in seedlings of *Hypericum perforatum* expression of *AOX2* was found to be stably low during the post-germinative phase (Velada et al. 2016). *AOX1* transcripts measured in the whole seedling without discriminating tissue-specific values increase in later stages in both *Arabidopsis* thaliana and *Hypericum perforatum*. *AOX1* was increased in *Arabidopsis thaliana* from 48 h after imbibition pointing to a differential role of both *AOX* genes. Nevertheless, the capacity of AOX was related to both AOX1 and AOX2 (Saisho et al. 2001). On the other side, cytochrome c oxidase mRNA levels increased continuously and corresponded to the increasing capacity of the COX pathway during germination and seedling growth. A bioinformatics search that we performed in recently published transcriptome data (Klepikova et al. 2016) underlines the importance of targeting tissue-specific transcription (Table 5.1). It confirms high expression of *AOX2* in dry seeds of *Arabidopsis thaliana* and also a rapid downregulation of *AOX2* early during germination, while *AOX1* genes and here especially *AOX1a* are simultaneously upregulated to the former high level of *AOX2*. This differential regulation of isoenzyme expression patterns might be linked to metabolite-specific control mechanisms through the change to an aerobic situation at germination (see in Costa et al. 2009). In dry seeds, fermentation is dominant (Botha et al. 1992), and the rate of CO_2 production is low (see Fig. 5.1), while after imbibition, mitochondria are activated. Whether there are differential impacts of both isozymes on the protective role of AOX against upcoming oxidative stress during mitochondrial respiration remains open. However, when seedling growth starts *AOX1* transcript levels explored at seedling meristems, cotyledons and hypocotyls are markedly decreased, and the lowest amount of *AOX* transcripts is found in the growing tissue, the seedling meristems (Table 5.1). This result is in

Table 5.1 Expression profile of alternative oxidase (AOX) genes of *Arabidopsis thaliana* in dry seeds, during seed germination, and in seedling tissues (meristem, cotyledons, hypocotyl, and root)

	Genes				
Conditions	*AtAOX1a*	*AtAOX1b*	*AtAOX1c*	*AtAOX1d*	*AtAOX2*
Dry seeds	33	2	0.00	33	2357
Germinating seeds 1 (first day after soaking)	155	0.39	99	0.39	216
Germinating seeds 2 (second day after soaking)	615	0.78	42	0.61	39
Germinating seeds 3 (third day after soaking)	2752	3	10	1	30
Seedling meristem	118	0.00	17	8	0.00
Seedling cotyledon	564	0.00	28	1	1
Seedling hypocotyl	767	0.00	0.00	5	0.00
Seedling root	511	0.00	4	3	3

agreement with former studies of Sieger et al. (2005) on transgene tobacco. These authors found that AOX1 regulates carbon use efficiency. They observed that increased AOX1 expression can be related to the suppression of growth. Suppression of yeast growth through AOX1 was observed also when yeast was transformed by the carrot *AOX1* gene depending on its concentration and a situation of mainly aerobic mitochondrial respiration (Arnholdt-Schmitt and Kumar Patil 2017). In summary, the available knowledge and presented bioinformatics data on respiration and respiration-related gene expression during germination allow hypothesizing that AOX genes can be interesting candidates for functional marker development linked to early steps in germination and to seedling growth. Recently, it was found that AOX might also have crucial function on optimizing structural interaction between plants and endophytes (Mercy et al. 2017), which can be especially important at seedling stage.

Data are read counts (derived from RNA-seq analyses) normalized by median-of-ratio method as described in Anders and Huber (2010). The data were accessed using the TRAVA (transcriptome variation analysis across different organs and developmental stages in *Arabidopsis*) webserver [http://travadb.org (Klepikova et al. 2016)] as well as the gene Ids of *AtAOX1a* (AT3G22370), *AtAOX1b* (AT3G22360), *AtAOX1c* (AT3G27620), *AtAOX1d* (AT1G32350), and *AtAOX2* (AT5G64210).

5.2 Conclusion

Seed germination efficiency and plant robustness are important for high-level and stable biomass production. For both traits, respiration plays essential role that links to evolutionary fitness as driver for biodiversity. Genetic variation in respiration traits can be explored to support sustainable agriculture with low chemical input. Calorespirometry is promising as a predictive functional tool to advance early plant selection for biomass production in conventional and molecular breeding. Genomics-based markers of any kind can be easily evaluated. Functional markers developed from *AOX* genes seem to be promising for improving biomass production. A vast number of studies across different species have been published during the last decade that indicate high genetic sequence variability in *AOX* genes (see publications at www.eu_chair.uevora.pt). Additional data from a diversity of species can be retrieved and explored from public and private data banks. The predictive power of calorespirometry can be used to validate whether AOX activity and *AOX* gene polymorphisms have relevant effects on biomass production.

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