Leaf Epinasty in Chrysanthemum: Enabling Breeding against an Adverse Trait by Physiological Research

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Abstract

Breeding for a certain trait is only possible when the phenotypic variation that is caused by genotypic variation can be estimated. For traits that strongly depend on environmental conditions, this can be extremely difficult and knowledge and collaboration with experts from other disciplines becomes essential. A well-known example is breeding for disease resistance. Here, we describe a similar approach to assist breeding against adverse leaf deformations that severely reduce the ornamental value of some chrysanthemum (*Dendranthema* × *grandiflora*) genotypes during greenhouse cultivation in winter. These leaf deformations occur rather unpredictably, but seem to be related to the increased use of assimilation light. To breed against this trait knowledge is needed (i) about inductive environments in which sensitive and insensitive genotypes are distinguishable, and (ii) about the physiological background associated with leaf epinasty. In this paper hypothetical physiological factors and mechanisms are discussed, which may mediate effects of light spectrum and greenhouse climate on leaf epinasty. One factor involved could be starch accumulation, since leaf epinasty usually aggravates after disbudding - a practice that most probably alters the sink-source balance. Additionally, light spectra can affect the circadian clock and thereby disturb starch synthesis and breakdown resulting in accumulation. Both within and independent of this process, plant hormones such as auxin and ethylene may play a role in leaf epinasty. This theoretical framework will be used to further investigate the physiological background of leaf epinasty and to come up with a test in which susceptibility for leaf epinasty can be assessed.

INTRODUCTION

Breeding for a certain trait is only possible when the phenotypic variation that is caused by genotypic variation can be estimated. In some traits, like most ornamental traits, this is easy to establish, since the trait hardly varies within the environmental range in which it is commonly grown. In others, like disease resistances, the environment plays a major and, in most cases, complicated role. This can make it difficult to breed for disease resistance, since inductive environments are often hard to establish and to keep constant. These complicated genotype environment interactions form a main reason why the breeder and phytopathologist collaborate: to make disease resistance assessment possible. Complicated environmental effects on the phenotype are not only reserved for disease resistance. In chrysanthemum there is also a morphological economically important trait that heavily varies within the typical growth circumstances. This is leaf epinasty: downward leaf curling along the transversal and longitudinal axes (Fukuda et al., 2008). In chrysanthemum it is observed in greenhouse production after disbudding (removing all flower buds except for the main bud), and during winter when assimilation

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lamps are used during long periods of the day. However, occurrence varies strongly per grower, growing season and genotype. Leaf epinasty reduces the effective photosynthetic area causing a decrease in light use efficiency (Meinen et al., 2009; Trouwborst et al., 2010). Next to that, it reduces ornamental value (Van Ieperen et al., 2008; Maaswinkel et al., 2011). To enable breeding against this trait, the plant physiologist acts where the plant pathologist acts to enable breeding for disease resistance: by providing underlying knowledge about inductive environments and the way plants respond to these environments.

More specifically, to enable breeding against leaf epinasty, knowledge is needed about (i) inductive environments close to typical growth practices in which sensitive and insensitive genotypes are distinguishable, and (ii) the physiological background associated with leaf epinasty. In this paper the major hypothetical physiological factors and their relations are treated that may mediate effects of light spectrum and greenhouse climate on leaf epinasty, in order to provide a theoretical framework for future research with the objective to make breeding against leaf epinasty possible.

LEAF EPINASTY AND LIGHT SPECTRUM

An interesting suggestion originating from growers' experiences is that leaf epinasty occurs mainly during winter. In greenhouse horticulture in The Netherlands it is very common to use high pressure sodium (HPS) lamps in winter, when outside light levels are low. The light spectrum of this lamp type differs a lot from sunlight. It has amongst others a much higher ratio between the amount of red and far-red light (R:FR), affecting phytochrome, and emits a relatively lower amount of blue light. Therefore, it is suggested that these light spectral characteristics may play a role in the occurrence of leaf epinasty. This is supported by earlier findings in geranium and *Arabidopsis*. When these plants were grown in only red light (which has an infinite R:FR) they showed severe leaf epinasty, and adding blue light inhibited the leaf epinasty (Fukuda et al., 2008; Inoue et al., 2008). These findings already suggest that growing chrysanthemum plants in monochromatic red light may induce leaf epinasty. However, it is unknown whether these phenomena have the same physiological background as what we see during practical growth circumstances in chrysanthemum. Next to that, it remains unsure what exact spectral characteristic is involved in the occurrence of leaf epinasty, the amount of blue light, or the R:FR. The added blue light in above mentioned experiments could have had an effect on both, since high blue light levels act as far red light on the state of phytochrome, inducing typical R:FR growth responses. Climate room experiments may give clarity on these uncertainties.

GENERAL HYPOTHESIS: INVOLVEMENT OF STARCH

Another suggestion from practice is that leaf epinasty occurs after disbudding. This is a practice in which all flower buds are removed except for the main bud. The lateral buds probably act as sinks; therefore, a disturbed sink-source relationship may be involved in formation of leaf epinasty (Van Ieperen et al., 2008; Maaswinkel et al., 2011). It was proposed that this disturbed sink-source relationship is expressed as starch accumulation. Also the other likely factor to affect leaf epinasty, light spectrum, may affect starch metabolism. The internal day-night rhythm, also known as the circadian clock, is regulated by light sensing of the phytochromes and cryptochromes (Devlin and Kay, 2000). Since HPS lamps deviate from normal sunlight in the spectral ranges absorbed by these two light receptors (the blue, red and far-red), this lamp type might disturb the circadian clock. Disturbance of the clock could result in starch accumulation, since this clock regulates starch breakdown and synthesis (Graf and Smith, 2011).

Leaf epinasty can be seen as a mechanism that reduces starch accumulation: as a result of the epinasty, the photosynthetic area is reduced resulting in a reduction of leaf photosynthesis and concomitant starch accumulation. Thus, in this hypothesis, lowering photosynthesis by leaf epinasty will eventually lead to a decrease of starch accumulation in leaves. A first pilot study under practical growth conditions seems to support this hypothesis, but the results were not fully conclusive (Maaswinkel et al., 2011).

INVOLVEMENT OF PHYTOHORMONES

Since phytohormones are involved in many physiological processes, it is very likely that these hormones also play important roles in above-mentioned relations. Both R:FR and the relative amount of blue light can have important effects on the production and transport of auxin (a.o. reviewed by Josse and Halliday, 2007). A nice example of how light affects auxin metabolism is the Cholodny-Went theory. This theory, originating already from the 1920s, describes the alteration of auxin transport and/or production when a shoot is exposed to a lateral blue light source. This causes phototropism: the ability of a plant to grow towards a light source. This process cannot explain directly the phenomenon of leaf epinasty, but indicates the tight relationship between light, auxin metabolism and differential growth. Next to that, the suggestion that auxin is involved is supported by findings that application of auxins exogenously could induce leaf epinasty (Keller and VanVolkenburgh, 1997; Jones et al., 1998; Keller and Van Volkenburgh, 1998; Keller, 2007) and that auxin-overproducing plants show a similar type of same leaf epinasty (Klee et al., 1987; Romano et al., 1993; Romano et al., 1995; Kim et al., 2007).

Ethylene is a second phytohormone that might be involved in leaf epinasty, for the main reason that it can cause differential growth, in terms of petiole epinasty (Jackson and Campbell, 1976; Reid et al., 1981; El-Iklil et al., 2000) or an exaggerated apical hook (Guzman and Ecker, 1990; Stepanova and Alonso, 2005). Other than affecting the sink-source balance, disbudding might enhance ethylene production, since plants are wounded which may cause an increase in ethylene production (Druege, 2006). This may be another approach to explain the occurrence after disbudding. Also light, and especially the R:FR, affects ethylene production: through the circadian clock (Rikin et al., 1984; Finlayson et al., 1998; Jasoni et al., 2002; Dziubinska et al., 2003; Thain et al., 2004), by production (Finlayson et al., 1998, 1999; Kurepin et al., 2007, 2010, 2011), and by sensitivity (Pierik et al., 2004).

CONCLUDING REMARKS

In this paper the possible physiological backgrounds of leaf epinasty are discussed; a relatively new research issue with a rather unorthodox interdisciplinary approach: the collaboration between plant physiologist and breeder to improve the breeding process. The information provides a framework and clues for future research directions with the objective to enable breeding against sensitivity to leaf epinasty. Potential areas of research lay amongst others in the effects of light quality, where extreme light spectra may induce leaf epinasty constitutively in sensitive genotypes, enabling selection. Other possible research subjects lay in the involvement of the phytohormones auxin and ethylene. Endogenous application and measurement of hormone production or content, may deliver interesting knowledge concerning the mechanisms behind occurrence of leaf epinasty.

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Figures

Fig. 1. Leaf epinasty in chrysanthemum. Left: normally shaped leaves, right: epinastic leaves.