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植物生物技术

本书文章选自 *Trends in Biotechnology, Trends in Genetics & Trends in Plant Science*

NEW FOCUS in
Life Sciences
生命科学新视野 4

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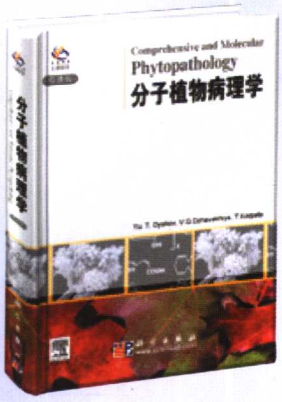

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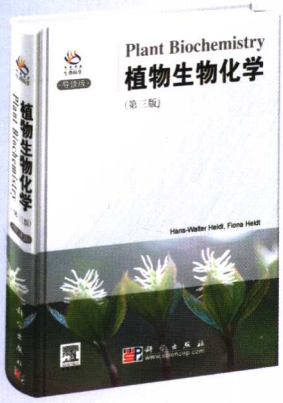
Comprehensive and Molecular Phytopathology

《分子植物病理学》（导读版）

原著：Yu.T.Dyakov, V.G.Dzhavakhiya, T.Korpela

本书收集了植物和病原体之间在分子水平“对话”的大量信息。而且还提供了大量反映植物与寄生物相互作用内在逻辑的数据。书中讨论了大量新发现，包括：寄主和非寄主抗性、特异和非特异性诱抗剂、诱抗剂和抑制剂以及植物和动物免疫。本书可以让读者了解如何预防疾病的发生，形成自己的植物—病原物互作的观点。

* 相比市场上其他书籍，提供了更多的内容
* 提供的了大量数据，使读者更好的理解寄主-寄生物的关系，揭示了病原性和抗性因子之间的内在关系。
* 讨论了植物-微生物之间的关系，以及植物-寄生物之间关系的分子研究方法
* 比较了植物免疫和动物免疫异同的研究历史



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Plant Biochemistry, 3e

《植物生物化学》第三版（导读版）

原著：Hans-Walter Heldt
导读：荆玉祥 研究员（中国科学院植物研究所）

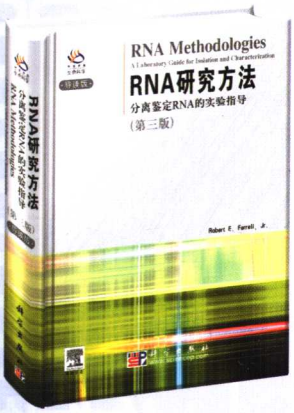
内容涵盖了植物生物化学的全部基础知识和前沿知识。

与以往的《植物生物化学》教科书不同，像氨基酸、碳水化合物及核酸的结构与功能、蛋白质的结构与功能、酶催化作用等基础生物化学知识都被有意略去，而只在对理解问题十分必要时才给予一定的介绍。因此本书是一本介于普通教科书与和专业教科书之间的折衷教材。

本书具有新颖性、前沿性。几乎在每一章节中均点出了研究的重点和热点。大到光合作用和固氮作用的信号传导、基因表达和网络调控，小到具体的蛋白，书中均点出了研究的最新进展、存在的不足和今后需要探索的方向。

本书综合性和比较性很强，不仅讲述了植物生物化学的多个领域，而且还与动物、微生物（包括病毒）生物化学进行了比较，使读者了解三者的相关知识，特别是三者在物质代谢方面的异同，拓展了生物化学的知识面，并加深了理解。

本书对于具备一定生物化学基础知识的学生和研究人员拓展知识和深入思考问题很有益处。



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RNA Methodologies, 3e

《RNA 研究方法》第三版（导读版）

原著：Robert E. Farrell, Jr.
导读：刘定干 研究员（中国科学院上海生命科学研究院生物化学与细胞生物学研究所）

本书作者是公认的 RNA 实验领域的专家，是著名的 Exon-Intron 生物技术培训中心的创立者。

本书汇集了有关 RNA（核糖核酸）的分子生物学和细胞生物学的各种实验方法，包括分离提取、纯化、鉴定、生物活性的检验，以及通过对细胞内 RNA 状态的分析研究细胞基因的转录及其调控等。这一版新增加了大约 30%的内容，涵盖了 RNA 研究的最新技术，比如 RNAi，生物芯片和生物信息技术等；另外对许多常规实验技术也进行了更新，比如 RT-PCR 新技术和改良技术、5′ 和 3′ RACE、消减 PCR 技术，以及 cDNA 的合成等。

该实验手册主要收集整理了最新的真核RNA分离及鉴定的相关方法，而对原核转录实验的介绍涉及较少。书中的实验方法均是经过试验验证的最优化的方法。全书都是围绕RNA这一中心问题展开的，每一部分都附有大量清晰的图片、表格，并且还有习题，可以帮助读者更有效地学习，也更有利于读者安排自己的试验。

虽然本书是一本实验指导书，所讲述的都是具体的RNA研究实验的方法，但它的读者绝不仅限于实际从事 RNA 实验的工作人员。许多在平时工作中也接触到 RNA 的概念，但是没有条件或很少有机会自己亲手进行 RNA 实验的人们，比如其他专业的科学工作者、工农业技术人员、中学生物学教师、临床医生、科普作家、科学出版物编辑、大学低年级学生，只要有阅读英文专业文章的能力，也可以翻阅这本书。这样能够补充自己知识的不足，了解分子生物学家们是怎样进行研究工作的，也能从中学到科学工作所必需的严格认真、实事求是的精神。

New Focus in Life Sciences

4

植物生物技术

生命科学新视野

1 中文摘要

植物生物技术

7 **Tuning the pores: towards engineering plants for improved water use efficiency**
L. Chaerle, N. Saibo and D. Van Der Straeten
调整通道：制造具有更高水利用效率的基因工程植物

15 **Transforming kelp into a marine bioreactor**
Song Qin, Peng Jiang and Chengkui Tseng
将海藻变成海洋生物反应器

20 **Bringing medicinal plants into cultivation: opportunities and challenges for biotechnology**
Peter H. Canter, Howard Thomas and Edzard Ernst
药用植物的种植——生物技术的机遇与挑战

26 **Using RNAi to improve plant nutritional value: from mechanism to application**
Guiliang Tang and Gad Galili
利用 RNAi 提高植物的营养价值——原理与应用

33 **Secondary plant metabolites in phytoremediation and biotransformation**
Andrew C. Singer, David E. Crowley and Ian P. Thompson
植物除污和生物转化中的植物次生代谢物

41 **The diversity of RNA silencing pathways in plants**
Peter Brodersen and Olivier Voinnet
植物中 RNA 沉默途径的多样性

54 ***Agrobacterium* T-DNA integration: molecules and models**
Tzvi Tzfira, Jianxiong Li, Benoît Lacroix and Vitaly Citovsky
农杆菌 T-DNA 整合：分子与模型

63 **Genetic engineering of wheat - current challenges and opportunities**
Prem L. Bhalla
小麦基因工程——目前的挑战和机遇

70 **Divide and conquer: development and cell cycle genes in plant transformation**
Renée S. Arias, Sergei A. Filichkin and Steven H. Strauss
分隔与征服：植物转化中的发育和细胞周期基因

77 **Global trends in plant transgenic science and technology (1973-2003)**
Philippe Vain
植物转基因科学和技术的全球趋势（1973-2003）

83 **Engineering drought and salinity tolerance in plants: lessons from genome-wide expression profiling in *Arabidopsis***
Katherine Denby and Chris Gehring
耐旱和耐盐的植物基因工程：拟南芥全基因组表达谱的启示

89 **Biopharmaceutical production in plants: problems, solutions and opportunities**
Véronique Gomord, Paul Chamberlain, Roy Jefferis and Loïc Faye
在植物中生产生物医学产品：问题、解决方案和机遇

96 **Engineering plants with increased disease resistance: what are we going to express?**
Sarah J. Gurr and Paul J. Rushton
制造具有更高抗病能力的基因工程植物：我们要表达什么？

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104 Engineering plants with increased disease resistance: how are we going to express it?
Sarah J. Gurr and Paul J. Rushton
制造具有更高的抗病能力的基因工程植物：我们怎样表达？

112 Genomics-based approaches to improve drought tolerance of crops
Roberto Tuberosa and Silvio Salvi
基因组学方法提高农作物的耐旱性

120 Identification, isolation and pyramiding of quantitative trait loci for rice breeding
Motoyuki Ashikari and Makoto Matsuoka
鉴定、分离和增加数量性状位点用于水稻育种

127 Potato in the age of biotechnology
Ewen Mullins, Dan Milbourne, Carlo Petti, Barbara M. Doyle-Prestwich and Conor Meade
生物技术时代的马铃薯

134 Golden Rice - five years on the road - five years to go?
Salim Al-Babili and Peter Beyer
黄金水稻——五年的历程及五年后的期待

143 Progress in the dissection and manipulation of vitamin E synthesis
Dean DellaPenna
维生素 E 合成的解析和操作进展

149 Plant-derived pharmaceuticals - the road forward
Julian K-C. Ma, Rachel Chikwamba, Penny Sparrow, Rainer Fischer, Richard Mahoney and Richard M. Twyman
植物源药物——前途无量

155 Volatile science? Metabolic engineering of terpenoids in plants
Asaph Aharoni, Maarten A. Jongsma and Harro J. Bouwmeester
挥发性的科学？ 植物萜类的代谢工程

164 Microarray expression profiling resources for plant genomics
Willem Albert Rensink and C. Robin Buell
用于植物基因组学研究的基因芯片表达谱资源

171 Developing salt-tolerant crop plants: challenges and opportunities
Toshio Yamaguchi and Eduardo Blumwald
耐盐农作物的开发：挑战和机遇

177 Genomics-assisted breeding for crop improvement
Rajeev K. Varshney, Andreas Graner and Mark E. Sorrells
用于作物改良的基因组学辅助育种

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植物生物技术

7 Tuning the pores: towards engineering plants for improved water use efficiency

Trends in Biotechnology, Volume 23, Issue 6, June 2005, Pages 308-315
L. Chaerle, N. Saibo and D. Van Der Straeten

调整通道：制造具有更高水利用效率的基因工程植物

21世纪社会面临的一个主要挑战是有限淡水资源的管理。农业用水占了人类消耗水量的三分之二，因此农业也是实现水资源更合理利用的一个主要领域。环境胁迫是限制稳定的粮食生产的主要因素。鉴于用于农作物水资源越发短缺，它也将成为国际农业经济的新兴要素。水资源缺乏问题的环境友好型和持久的解决方案是：在采用更有效的灌溉方式的同时，种植那些具有最佳水利用效率的高产农作物，而这些农作物可以通过基因工程或传统的育种方式得到。

15 Transforming kelp into a marine bioreactor

Trends in Biotechnology, Volume 23, Issue 5, May 2005, Pages 264-268
Song Qin, Peng Jiang and Chengkui Tseng

将海藻变成海洋生物反应器

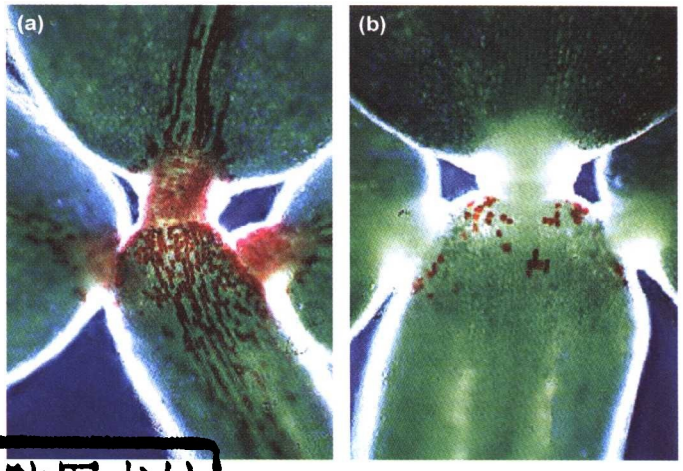
过去十年，人们对多种海藻进行了基因工程研究。到目前为止，人们已经对多种海藻，包括红海藻 *Porphyra*、*Gracilaria*、*Grateloupia*、*Kappaphycus*、*Ceramium* 和绿海藻 *Ulva* 进行了遗传转化研究。基于陆生植物的转化技术，人们通过对海藻生活周期的调整，在培养最常用的褐海藻 *Laminaria japonica* 上建立了一种遗传转化的模式系统。这个模式系统在利用转基因海藻生产有价值的产品方面很有潜力；考虑到生物安全的因素，还建议建立一个转基因海藻的室内培养系统。在这篇综述中，将介绍如何使用海藻转化的模式系统，并将重点探讨把海藻作为一个海洋生物反应器应用的可能性。

20 Bringing medicinal plants into cultivation: opportunities and challenges for biotechnology

Trends in Biotechnology, Volume 23, Issue 4, April 2005, Pages 180-185
Peter H. Canter, Howard Thomas and Edzard Ernst

药用植物的种植——生物技术的机遇与挑战

目前草药的利用越来越普遍，消费量也在不断上升。野生的草药是草药原材料的主要来源，但也导致遗传多样性的损失以及生境的破坏。人工培育是一个可行的替代方法，可以克服草药提取物的问题，诸如草药辨识错误、遗传和表型的变化、提取物的变化和不稳定性、毒性成分和污染物等。利用可控的环境条件可以克服草药培育的困难，这可以成为一种对因生物活性化合物和毒素而产生的不同表型进行操作的方法。传统的植物育种方法可以改善农艺特性和药学特性，而分子标记辅助选种方法也将得到越来越多的应用。通过组织培养和遗传转化改变代谢途径来生产目标代谢产物方面，人们已经取得了长足的进步。而阻碍药用植物成功进行商业种植的因素包括很难预测哪种提取物适于市场化，而且市场更偏爱天然提取物。

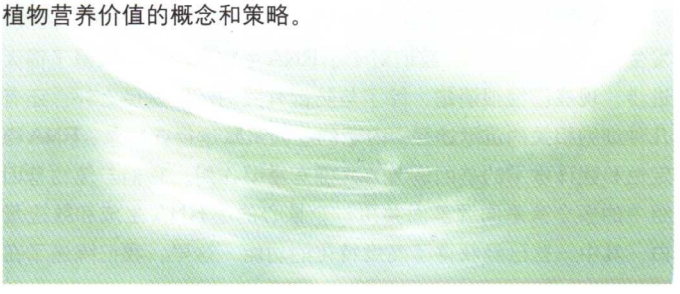


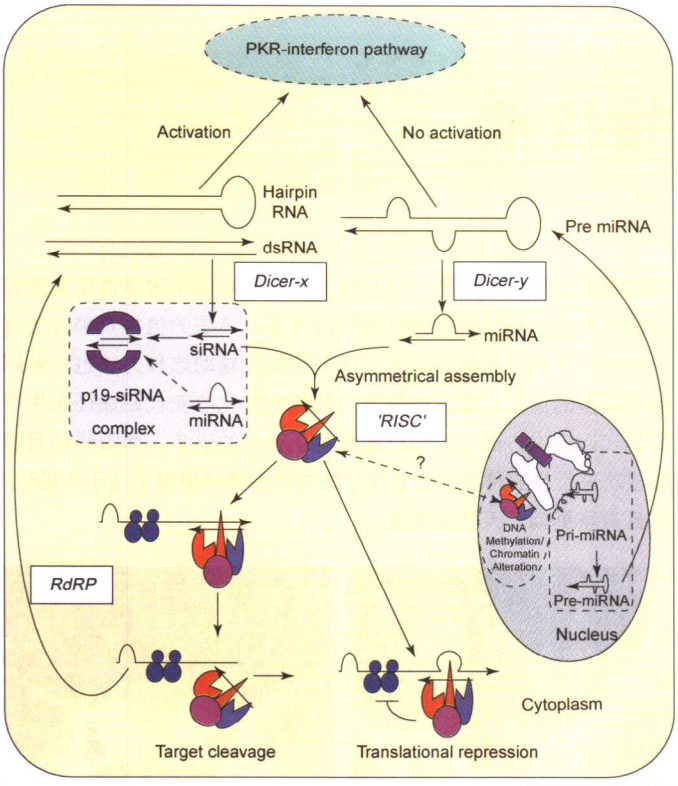
21 Using RNAi to improve plant nutritional value: from mechanism to application

Trends in Biotechnology, Volume 22, Issue 9, September 2004, Pages 463-469
Guiliang Tang and Gad Galili

利用RNAi提高植物的营养价值——原理与应用

RNA干扰（RNAi）是基因抑制的一个古老机制，但是目前人们并没有完全了解其机理及生物学功能。很多研究的焦点都集中在开发RNAi技术来治疗人类疾病以及提高植物的性状上。但是，在利用RNAi技术提高植物对人类和动物的营养价值，以及开发相关的RNAi技术方面，目前还处于起步阶段。在这里我们讨论当前人们对植物RNAi功能的认识，以及通过开发植物RNAi技术提高植物营养价值的概念和策略。





TRENDS in Biotechnology

33 Secondary plant metabolites in phytoremediation and biotransformation

Trends in Biotechnology, Volume 21, Issue 3, March 2003, Pages 123-130

Andrew C. Singer, David E. Crowley and Ian P. Thompson

植物除污和生物转化中的植物次生代谢物

几千年来，植物一直用次生代谢物来对付微生物、昆虫，同样也对付人类，最终产生出一个从共生到致病的兼性与专性相互作用的复杂而动态的混合体。植物的次生代谢产物在合成降解自然界中发现的多种有机污染物酶的方面具有重要作用。有关植物次生代谢产物和酶的多样性之间的关系还需要进行进一步探索，这在诸如有害物的控制、生物除污，以及精细化工产品生产方面具有潜在的应用价值。

41 The diversity of RNA silencing pathways in plants

Trends in Genetics, Volume 22, Issue 5, May 2006, Pages 268-280

Peter Brodersen and Olivier Voinnet

植物中 RNA 沉默途径的多样性

在植物中发现的 RNA 沉默机制是，通过小（20-26 nt）而同源 RNA 分子发生作用使侵入的核酸（如转入的基因和病毒之类）发生沉默。最近几年，我们对于小 RNA 生物学的认识取得了很大进步，现在已经很清楚：除了与防御有关的沉默途径之外，还有几种细胞相关的沉默途径。内源的基因沉默途径在转录、RNA 稳定性和翻译水平的基因调节方面都有重要作用。它们与植物基因组中的多个旁系同源基因共用一个核心的小 RNA 生成和效应蛋白，其中一些已经获得了高度特化的功能。这里，我们综述了在植物 RNA 沉默领域中的最新进展，包括已经鉴定的特定沉默途径的元件和植物中愈加清晰的 RNA 沉默机制及生物学意义。

54 *Agrobacterium* T-DNA integration: molecules and models

Trends in Genetics, Volume 20, Issue 8, 1 August 2004, Pages 375-383

Tzvi Tzfira, Jianxiong Li, Benoît Lacroix and Vitaly Citovsky

农杆菌 T-DNA 整合：分子与模型

由农杆菌介导的基因转化包括 DNA 分子（T-DNA）从细菌向真核宿主细胞的转移，及其整合入宿主基因组的过程。尽管已经有大量的研究揭示出农杆菌与植物间的细胞转运及农杆菌T-DNA进入细胞核的机制，随后的整合过程仍不甚了解，虽然人们已经提出了不同的整合机制模型。最新的基因和功能研究揭示了参与 DNA 修复和维持 T-DNA 整合的寄主蛋白的重要性。本文中，我们将综述对于这些蛋白特异功能的了解，并提出一个详细的整合模型。

63 Genetic engineering of wheat - current challenges and opportunities

Trends in Biotechnology, Volume 24, Issue 7, July 2006, Pages 305-311

Prem L. Bhalla

小麦基因工程——目前的挑战和机遇

小麦是世界范围种植的主要粮食作物之一。然而，谷类作物的产量不能满足日益增长的人口数量。单是要满足不断增长的需求，小麦产量就需要有大幅度的提高（2020年之前增加40%）。然而，由于可用的基因库有限，传统的植物育种手段很难实现这个增长。应用 DNA 重组技术来提高小麦的质量和产量不仅值得尝试，而且还可能创造出新的机遇。尽管用于改善这些性状的基因转化技术开发已经取得了巨大进展，但小麦基因转化依然是植物生物技术的一个重要挑战。将基因组时代的潜能应用到小麦育种面临许多障碍，包括需要培育不带可选择标记的小麦优良品种，引入尽量少的或者没有基因间的 DNA，以及关于基因改良食品的社会和市场问题等。

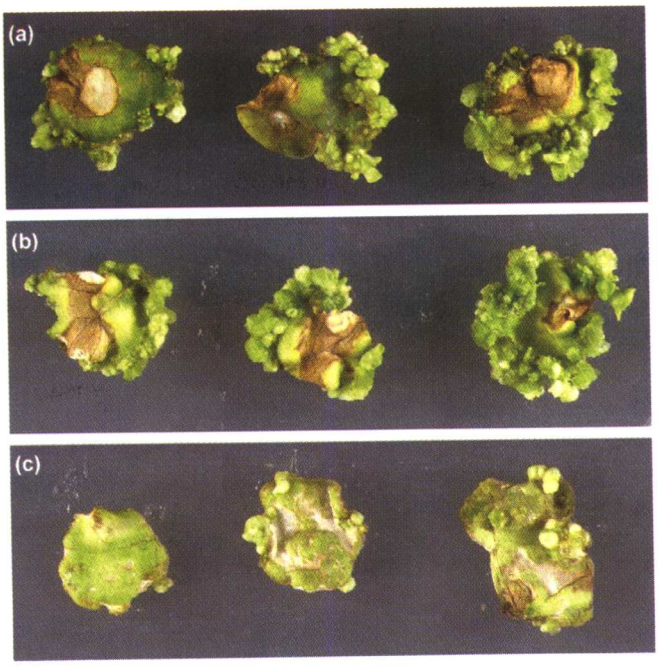
70 Divide and conquer: development and cell cycle genes in plant transformation

Trends in Biotechnology, Volume 24, Issue 6, June 2006, Pages 267-273

Renée S. Arias, Sergei A. Filichkin and Steven H. Strauss

分隔与征服：植物转化中的发育和细胞周期基因

对多种植物物种来说，基因转化和转基因植物的再生仍然不可行。我们认为，通过改变染色质结构和利用表观遗传方法控制基因表达，可以对控制细胞周期和发育的基因进行可诱导表达或抑制，这有可能充分提高转化和再生的能力。转化效率在细胞核处于 S 期和 G2 期时比较高，而操控那些激活或沉默促进 G1-S 转型的基因，能够同时提高瞬时转化率和稳定转化率。用 RBR 和 VIP1 直接或者通过 IPT 和 ESR 调节激素来间接控制细胞周期，已经可以提高稳定转化率。其他那些可促进 DNA 整合或细胞多能性



的靶基因还包括HP1, CycD3和CycD1。大量的EST数据库、完整的植物基因组序列和可诱导基因表达系统，为通过检验同源基因来提高转化和再生能力提供了可能性。

77 Global trends in plant transgenic science and technology (1973-2003)

Trends in Biotechnology, Volume 24, Issue 5, May 2006, Pages 206-211
Philippe Vain

植物转基因科学和技术的全球趋势（1973 – 2003）

转基因科学和技术是植物分子遗传学和转基因作物改良尖端技术的基础。了解该领域的规模和增长对科学家、各国或国际的研究机构、资助机构和政策制订者们都很重要。由于对转基因技术尚存在争论，所以这种了解对整个社会也非常重要。过去30年文献的统计分析表明，转基因科学近十年在亚洲有了显著增长，在北美得到持续发展，而最近在世界其他地区发展放缓。不计中国和印度的产出，从20世纪90年代早中期开始，集中在转基因技术开发方面的论文已经在世界范围内减少。这个趋势与转基因作物相关研究的增加相反。

83 Engineering drought and salinity tolerance in plants: lessons from genome-wide expression profiling in *Arabidopsis*

Trends in Biotechnology, Volume 23, Issue 11, November 2005, Pages 547-552
Katherine Denby and Chris Gehring

耐旱和耐盐的植物基因工程：拟南芥全基因组表达谱的启示

世界食品安全越来越依赖于对作物的不断改良，尤其是农作物抗旱和抗盐性的增强。模式植物拟南芥的基因组完全测序，全基因组微阵列芯片的开发，加上越来越多的公共数据和分析工具，这些都为在全基因组水平上系统分析植物对逆境的响应开辟了新的道路。这里我们将列举一些范例，展示全基因组表达谱将如何帮我们理解复杂的逆境响应反应，以及对那些可能开发出商品化的可持续发展的农作物新转基因进行鉴定评估。

89 Biopharmaceutical production in plants: problems, solutions and opportunities

Trends in Biotechnology, Volume 23, Issue 11, November 2005, Pages 559-565
Véronique Gomord, Paul Chamberlain, Roy Jefferis and Loïc Faye

在植物中生产生物医学产品：问题、解决方案和机遇

植物和哺乳动物N-连接的多糖之间在结构上存在很大的区别，那些植物多糖对大多数实验哺乳动物具有免疫原性，把它们通过非肠道方式注射入人体可刺激产生多糖特异的IgE及IgG抗体。然而，由于人在饮食中经常接触植物糖蛋白，所以通过植物生产的糖基化药品（pharmaceuticals, PMPs）可以用于局部使用和口服。为了全面开发植物生产非肠道用药的药物蛋白的潜力，可能有必要通过抑制植物特异的翻译后修饰来得到“人源化”的非免疫原性N-连接糖蛋白的PMPs。相对于哺乳动物细胞培养，植物生产药品的成本更低，同时还可以降低哺乳动物病原菌传播的风险。

96 Engineering plants with increased disease resistance: what are we going to express?

Trends in Biotechnology, Volume 23, Issue 6, June 2005, Pages 275-282
Sarah J. Gurr and Paul J. Rushton

制造具有更高抗病能力的基因工程植物：我们要表达什么？

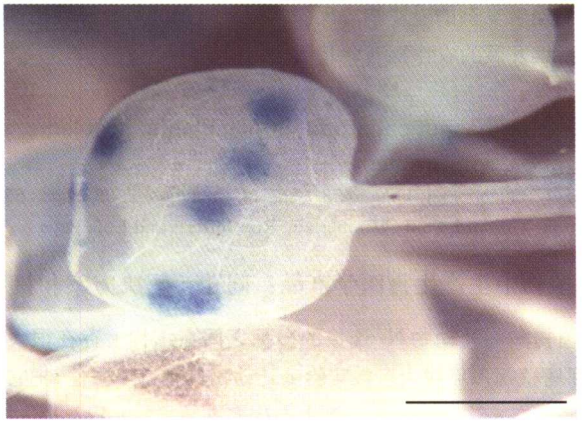
通过转基因技术来制造具有更高更持久抗病性的植物，我们必须回答两个问题。首先，我们通过表达哪个或哪些基因来提高抗病能力，其次是我们如何表达这些基因，使农作物的产量得到切实提高？新兴的技术为我们提供了很多候选基因，这些基因可以通过基因工程来增强农作物的防护能力。这些基因可能来自植物、病原菌或其他生物，而且几种基因操作的策略已初显成效。这里我们将讨论持续抗病植物的近期研究进展以及未来发展展望。

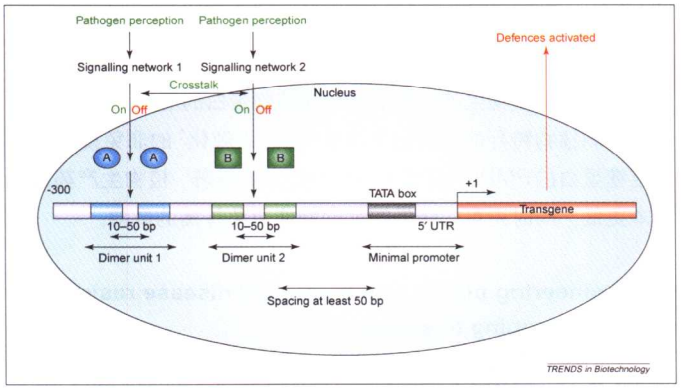
104 Engineering plants with increased disease resistance: how are we going to express it?

Trends in Biotechnology, Volume 23, Issue 6, June 2005, Pages 283-290
Sarah J. Gurr and Paul J. Rushton

制造具有更高的抗病能力的基因工程植物：我们怎样表达？

转入基因的精确控制对于制造具有更高抗病能力的植物是至关重要的。许多早期提高抗病能力的尝试都是组成型过量表达防卫基因，但往往都导致植物的品质变差。现在已经很清楚的是，如果不受控的防卫反应在未被侵染的细胞中被激活的话，由防卫反应引起的大范围细胞重编程将会造成产量降低。因此运用病原诱导的启动子可能是最有效的策略，因为它们可以通过把防卫基因的表达限制在被侵染的细胞来降低抗性的成本。尽管目前由于缺少合适的启动子使得这方面的研究进展受阻，但是新的研究将会揭示更多可能有用的天然启动子。另外，人们在“设计”启动子的研究中也取得了令人鼓舞的结果。





112 Genomics-based approaches to improve drought tolerance of crops

Trends in Plant Science, Volume 11, Issue 8, August 2006, Pages 405-412

Roberto Tuberosa and Silvio Salvi

基因组学方法提高农作物的耐旱性

植物在分子、细胞及发育水平上对干旱反应的遗传机制，涉及到很多受水调控的基因。基于基因组学的方法，我们可以找到那些影响这些反应的数量性状基因座(QTLs)中的农艺性状等位基因，使我们可以更有效地提高农作物在缺水环境中的耐干旱能力和产量。分子标记辅助育种方法已在帮助育种学家们改善作物与干旱相关的性状。对基因序列和基因产物的分析将有助于我们鉴定和克隆到那些位于数量性状位点上的基因。基于上述前提，我们有理由相信可以在很短的时间内从遗传和功能两个角度拓宽对植物抗旱机理的认识。通过“人为设计”，“裁剪”新的基因型，这将产生新的表型。但要真正发挥这种基因组学辅助育种方法的潜力，还需要一个多学科的方法，以及对影响对耐旱性的分子和生理学过程有一个整体的认识。

120 Identification, isolation and pyramiding of quantitative trait loci for rice breeding

Trends in Plant Science, Volume 11, Issue 7, July 2006, Pages 344-350

Motoyuki Ashikari and Makoto Matsuoka

鉴定、分离和增加数量性状位点用于水稻育种

很多重要的农艺性状都是由被称为数量性状位点(QTLs)上的数个基因控制的。长期以来分离鉴定重要的由数量性状位点控制的农艺性状都很困难，因为它们的遗传特性很复杂。但是，水稻全基因组序列测序工作的完成大大推动了数量性状位点的克隆以及累加育种工作。由于数量性状位点产生于自然变异，所以利用更大范围内的变异（比如说一些在野生种内发现的变异）就显得尤为重要了。另外，使用起源于野生种的渐渗系(Introgression Lines, ILs)，结合标记辅助选择将大大促进基因的有效鉴定。本综述将系统地描述近些年来在水稻数量性状位点研究中的进展，其中包括数量性状位点作图、克隆和累加。

127 Potato in the age of biotechnology

Trends in Plant Science, Volume 11, Issue 5, May 2006, Pages 254-260

Ewen Mullins, Dan Milbourne, Carlo Petti, Barbara M. Doyle-Prestwich and Conor Meade

生物技术时代的马铃薯

目前，为了增强和扩大传统马铃薯在食品生产中的比重，生物技术已经得到了广泛地应用。例如，通过修饰其功能，利用马铃薯来生产医药或工业化合物已经成为现实，而且马铃薯的抗病能力也得到根本性地提高。在拓宽马铃薯作用方面有两个关键性的进展，其一是近期在马铃薯结构和功能基因组研究领域的进展，其二是把人们感兴趣的基因转入马铃薯基因组的能力。本文我们将讨论这两方面的进展是如何使马铃薯产品多元化的。

134 Golden Rice - five years on the road - five years to go?

Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 565-573

Salim Al-Babili and Peter Beyer

黄金水稻——五年的历程及五年后的期待

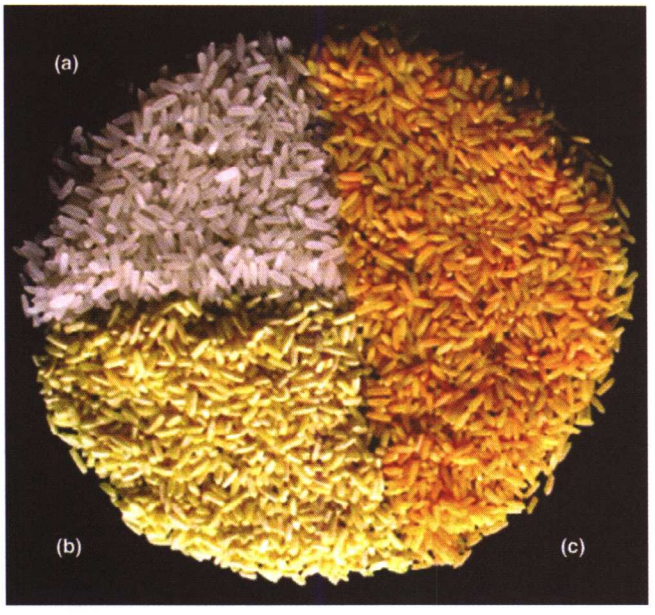
在金米（Golden Rice）的谷粒中积累维生素原 A 是遗传转化的结果。在维生素 A 普遍缺乏的发展中国家，人们期望金米可以通过农业来持续提供这种重要的微量营养元素。自金米投入生产以来，人们已对原型金米进行了大量的深入研究以提高维生素 A 的含量，建立补充类胡萝卜素的科学基础，以更好地符合安全法规的要求。目前，关注的焦点是如何将这些金米有效地交到农民的手中。这是在国际研究协会的帮助下开展起来的一种全新的公共部门研究的途径。除此之外，进一步提高金米营养价值的研究也正在进行。

143 Progress in the dissection and manipulation of vitamin E synthesis

Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 574-579
Dean DellaPenna

维生素E合成的解析和操作进展

Tocochromanols是一组包含四种生育酚和四种生育三烯酚的物质，它们共同构成了人类饮食的必须营养成份——维生素E。Tocochromanols只在好氧的光合生物中合成。虽然在体外它们具有类似的抗氧化活性，但在体内单个的tocochromanols之间的维生素E活性差异却很大。在过去的几年中，通过对模式生物尤其是拟南芥和蓝藻PCC6803突变体和转基因的研究，几乎所有核心途径基因都得以分离和研究。通过这些基因改造的代谢途径对于我们了解植物对tocochromanol合成的分子遗传和生化调控具有重要意义。产生的知识正努力推动对这种主要作物中的重要营养物水平的操作，以造福发达国家和发展中国家的人民。



149 Plant-derived pharmaceuticals - the road forward

Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 580-585
Julian K-C. Ma, Rachel Chikwamba, Penny Sparrow, Rainer Fischer, Richard Mahoney and Richard M. Twyman

植物源药物——前途无量

植物源药物即将成为下一个在生物技术领域的主要商业增长点。植物源药物在生产规模、经济性、产品安全、储存和运输的便捷性等方面都具有任何现有商业化系统所不能比拟的优点。同时它还创造了向发展中国家供应低价药物和疫苗的条件。然而，虽然有诸多的优点，植物源药物的商业化却被不明确的管理条例所限制，特别是要用GMP的标准对田间生长的植物进行管理。这类产品的成功还取决于知识产权方面的多方磋商，尤其是能否获得可以在发展中国家自由操作的许可。

155 Volatile science? Metabolic engineering of terpenoids in plants

Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 594-602
Asaph Aharoni, Maarten A. Jongsma and Harro J. Bouwmeester

挥发性的科学？ 植物萜类的代谢工程

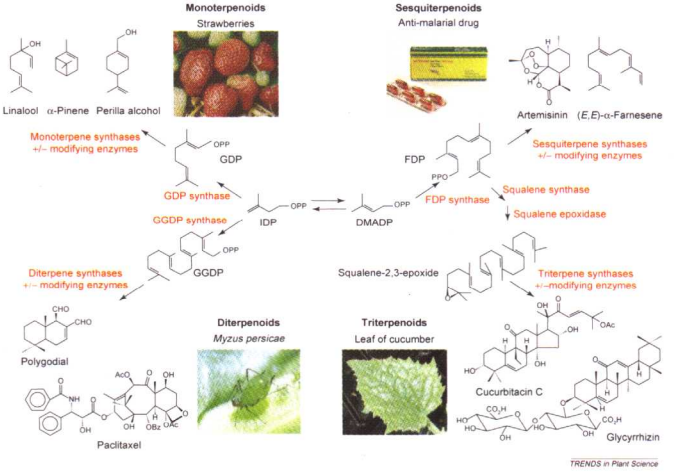
萜类对植物的生存是重要的，在人体内它们同样行使有益的生物学功能。在这篇综述中，我们描述了萜类代谢工程中的尖端技术，展示了在过去短短几年中该领域所取得的重大进展。相关酶类的亚细胞定位显示了萜类前体在亚细胞区域中并不是像先前想象的那样严格分开的，这就使得人们能对代谢途径中跨细胞区室的多个步骤进行工程改造。那些经过改造的植物表明了昆虫的行为受萜类的影响。我们期望人们将在植物生产萜类的工程改造方面取得快速进展。这些转基因植物除了商业方面的价值外，还可以加深人们对这些挥发性次生代谢产物生物学功能的了解。

164 Microarray expression profiling resources for plant genomics

Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 603-609
Willem Albert Rensink and C. Robin Buell

用于植物基因组学研究的微阵列表达谱资源

在过去的十年中，人们对几种植物的深入研究产生了大量的基因组数据，包括基因组水平的序列数据和功能注释数据。人们用各种技术，诸如表达序列标签（ESTs）、大规模平行特征测序（MPSS）以及微阵列等来研究基因的表达，试图同时提供很多基因的功能数据。这篇综述将集中介绍近年来关于微阵列在植物基因组研究中的应用进展，以及现有的基于微阵列的植物基因表达数据库。大量的拟南芥微阵列数据可以免费获取。最近发展起来的芯片平台可用于收集一些农作物的基因组表达谱数据。这些平台产生了一些公共数据库，人们从中可以获取大规模的表达数据，这些数据可以用于基因功能的研究。



171 Developing salt-tolerant crop plants: challenges and opportunities

Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 615-620

Toshio Yamaguchi and Eduardo Blumwald

耐盐农作物的开发：挑战和机遇

土壤盐碱化是全球大部分土地所面临的问题，它是导致作物产量降低的主要非生物胁迫之一。培育耐盐作物的需求是不言而喻的。现有两种主要的途径用于提高作物的耐盐性：(1) 通过逆境下直接筛选，或者通过对数量性状作图以及随后的标记辅助的筛选来发掘自然的遗传变异；(2) 通过导入新的基因或是改变已有基因的表达水平来获得转基因耐盐作物。在这篇综述中，我们讨论了近年来人们在开发耐盐作物时所遇到的挑战和机遇。

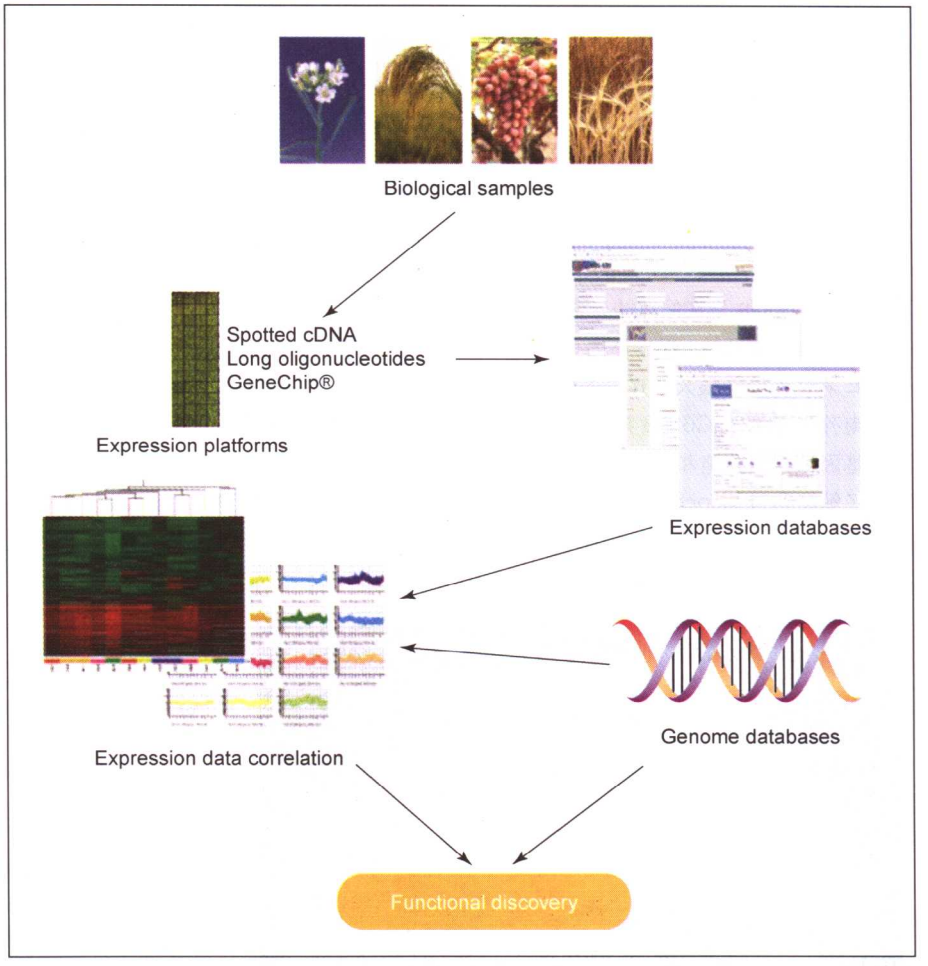
177 Genomics-assisted breeding for crop improvement

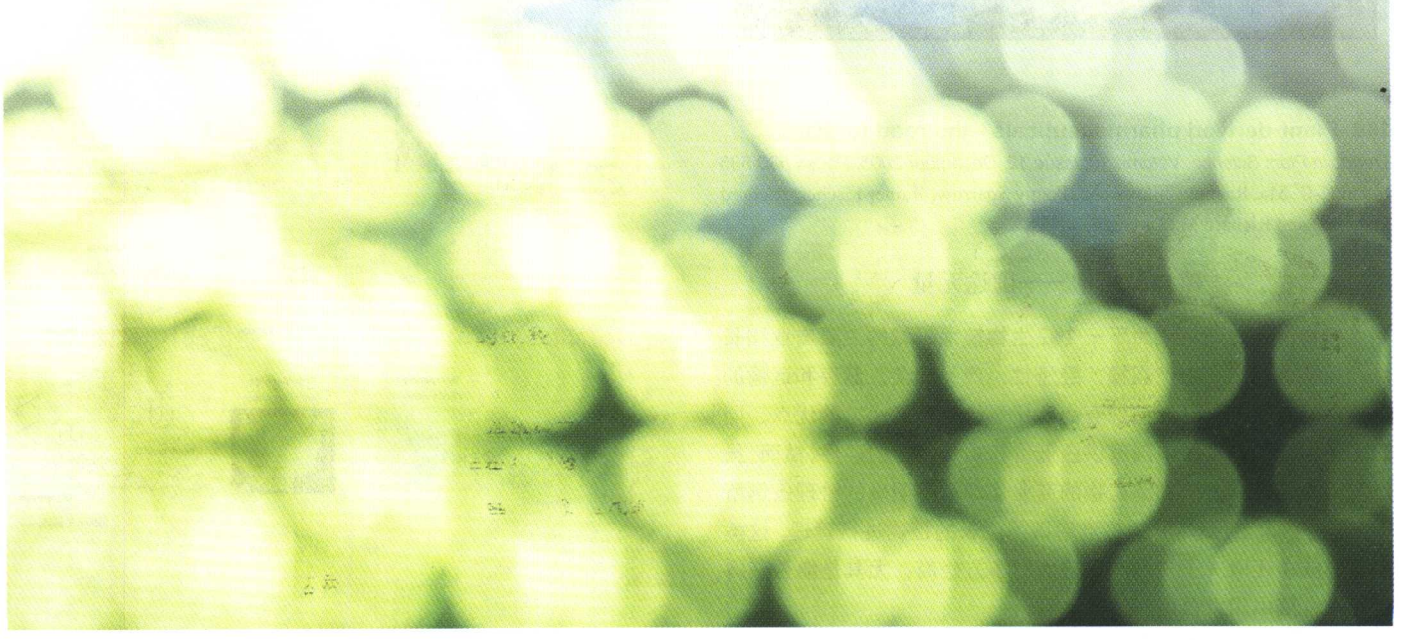
Trends in Plant Science, Volume 10, Issue 12, December 2005, Pages 621-630

Rajeev K. Varshney, Andreas Graner and Mark E. Sorrells

用于作物改良的基因组学辅助育种

基因组学研究中产生了诸如功能性的分子标记以及信息学之类的新工具，此外还有关于统计学和遗传现象的新知识，这些都可以提高作物改良效率和精确性。尤其是在阐释杂种优势和表观遗传学的基本机制以及如何进行操作等方面具有巨大的潜力。将来，根据对种群中所有独立分离的等位基因相对效应强弱的认识，育种者可以在芯片上设计一种基因型来进行全基因组的筛选。目前，高额的投入限制了基因组学辅助育种的应用，特别是对一些近自交和较小的作物。尽管如此，标记辅助育种和筛选将会逐渐演变为基因组学辅助育种。





Tuning the pores: towards engineering plants for improved water use efficiency

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The management of limited fresh water resources is a major challenge facing society in the 21st century. The agricultural sector accounts for more than two-thirds of human water withdrawal and is therefore a prime area to implement a more rational water use. Environmental stresses are a major factor limiting stable food production. Given the growing shortage of available water for crops this will be an emerging factor in international agricultural economy. The most environmentally friendly and durable solution to the problem of water shortage is to complement more efficient irrigation approaches with crops with optimal water use efficiency, achieved either through genetic engineering or conventional breeding, combined with high yields.

Introduction

Plant leaves and stems have microscopic epidermal pores flanked by a pair of guard cells, called stomata, which enable gas exchange – mainly of water vapour and carbon dioxide – between inner leaf tissues and surrounding air. Environmental cues, such as light intensity, light quality, water status, temperature and the concentration of atmospheric carbon dioxide (which influences the leaf internal CO_2 concentration C_i), and also endogenous (mainly hormonal) signals, control the development, density and aperture of stomata [1,2]. These factors influence both water loss by transpiration and net photosynthesis. Water use efficiency (WUE) is therefore defined as CO_2 assimilation per unit water transpired. Although reducing transpiration by stomatal closure is the most prominent response to drought, it could also be optimized through the control of stomatal size and density [3].

Here we present an overview of recent advances in understanding stomatal development and response, which determine the actual gas exchange capacity of a plant and have an important impact on its final yield. In addition, we highlight major achievements in enhancing dehydration tolerance in plants. Finally, we illustrate how imaging technology can help in the process towards engineering high yield crops tolerant to limited water supplies.

Environmental control of stomatal development

Despite the fact that several genes involved in stomatal development have been characterized (**Box 1**), little is known about the environmental control thereof. In most species, an increase in CO_2 results in a lower stomatal density [3,4]. The *Arabidopsis* gene *HIC (high carbon dioxide)* was the first gene to be identified belonging to a signaling pathway that controls stomatal development in response to an environmental cue [5]. *HIC* codes for an enzyme involved in the synthesis of very-long-chain fatty acids and is a negative regulator of stomatal development in response to CO_2 concentration. The *hic*$^-$ phenotype is not different to wild type except when grown in elevated CO_2, in which case the mutant shows a higher stomatal index (relative prevalence of stomatal cells). This suggests that the epidermal wax (very-long-chain fatty acid derivatives) composition of the cuticle of the guard cells controls stomatal numbers at elevated CO_2 [4]. Furthermore, plants show a more pronounced response (lower stomatal density) to high CO_2 under drought conditions, compared with well-watered plants [3], suggesting that CO_2 and drought signaling might interact. Whether HIC has a role in the transduction of other external signals towards stomatal development remains to be determined [6]. Plants grown at low humidity have an increased cuticle wax load [6] and a lower stomatal density than those grown at higher humidity [7]. Moreover, it was shown that mutants with enhanced wax load and altered wax composition show a lower stomatal index and higher drought tolerance [8], indicating that cuticle wax composition might also be involved in the control of stomatal development by water status. Other environmental cues, such as salt stress, also result in a reduction of stomatal index [9].

Mitogen-activated protein kinases (MAPK) have been suggested to integrate responses to stress, growth and cytokinesis [10]. The requirement for YODA (YDA) in meristemoids (**Box 1**) might reflect the use of MAPK signaling in response to a changing environment [11]. Hence, YDA might have an important role in drought-induced stomatal development. Furthermore, overexpression of protein kinases (such as SRK2C and NPK1 [12,13])

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Box 1. Stomatal development (Figure I)

Stomata develop from meristemoid mother cells (MMC), which divide asymmetrically to form a nonstomatal subsidiary cell (SC) and a smaller cell that becomes a meristemoid (M) [60]. The meristemoid divides asymmetrically 1–3 times and then differentiates into a guard mother cell (GMC), which produces two guard cells (GC). Stomata formation follows strict spacing rules, leaving at least one pavement cell in between two stomatal complexes. The first stomatal patterning mutants isolated were *too many mouths* (*tmm*) and *four lips* (*flp*), showing clustered stomata (i.e. stomata that are not separated by intervening pavement cells) in the cotyledons [60]. TMM, a putative cell surface receptor, participates in a signaling pathway that controls the plane of patterning divisions as well as cell proliferation and differentiation based on a positional context [61,62]. FLP limits the cell division competence of the GMCs, acting only in later stages of the meristemoid pathway [60]. A third mutant that exhibits increased stomatal density and formation of clustered stomata was designated *sdd1 (stomatal density and distribution1)* [63]. SDD1 acts through control of cell fate and orientation of cell divisions. SDD1 is a predicted subtilisin-like protease, probably modifying extracellular ligands that bind to TMM and a co-receptor kinase. It was suggested that SDD1 is less important for the one-cell spacing pattern than TMM but is more crucial for determining stomatal density [7,60,62].

Recently, a cell-fate switch in stomatal development was identified and designated YODA (YDA). YDA is a newly characterized mitogen-activated protein kinase kinase kinase (MAPKKK) acting as a negative regulator of stomatal development [11,20]. Genetic analysis places YDA downstream of TMM and SDD. YDA might alternatively act in an independent pathway controlling cell fate in the same uncommitted cells as TMM and SDD – before GMC specification [11]. YDA acts before FLP. A putative transcription factor named FAMA is also involved in stomatal patterning and development. A corresponding T-DNA insertion line shows no stomata [11]. Whether FAMA is a target for MAPK signaling remains to be determined.

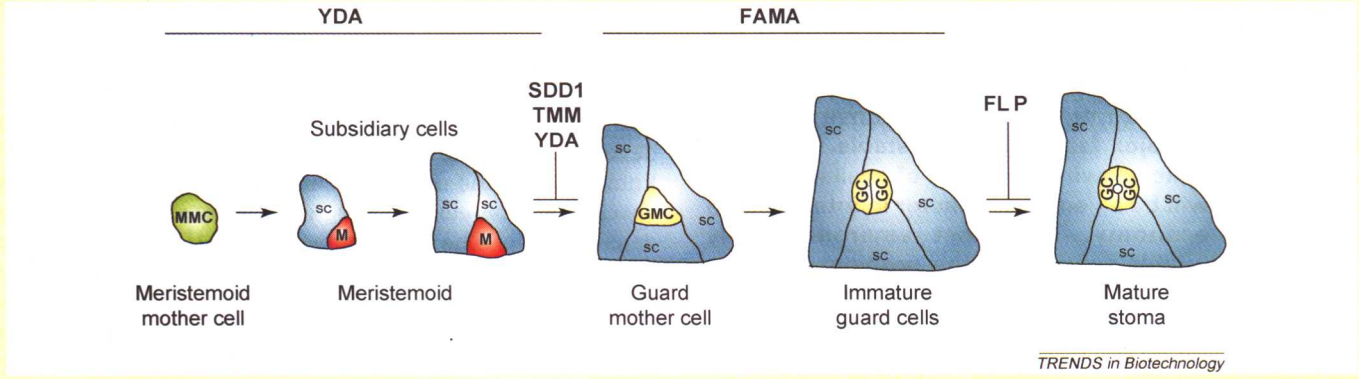

Figure I. Stomatal development.

resulted in enhanced dehydration tolerance confirming their implication in the regulation of water usage. In addition, plants overexpressing other genes involved in drought tolerance, for example, the transcription factor CBF4, might display changes in stomatal control or development [14].

The role of the plant growth regulator abscisic acid (ABA) on stomatal development in plants exposed to drought is still not clear. ABA-treated *Tradescantia virginiana* plants had significantly smaller stomata and higher stomatal density in their lower epidermis, compared with non-treated plants [15]. These characteristics might enhance WUE in drought conditions. Small stomata can open and close more rapidly and thus provide the capacity for a rapid decrease in stomatal conductance of a leaf, minimizing water loss upon drought [16]. In *Arabidopsis,* the stomatal index of wild-type and ABA-insensitive or ABA-deficient mutants was similar [17]. This suggests that ABA does not have an essential role in stomatal development in normal environmental conditions; however, it does not imply that ABA is unnecessary for stomatal development under stress conditions. Besides ABA, ethylene is a signal implied in many stress responses known to affect stomatal development [18,19].

Stomatal responses to drought

Stomatal pore opening and closure are regulated by environmental signals. This is a short-term adaptation that enables plants to retain water upon drought and maximize CO_2 uptake – essential to photosynthesis – during the day (Box 2) [20]. At night, stomatal aperture decreases. The efficiency and speed of stomatal movement to fluctuating water availability [influenced by the water vapor pressure deficit (VPD) between the leaf and surrounding air] are major factors in maximizing photosynthesis and WUE [21,22]. To alleviate the ever-increasing water demand of agriculture, more water-efficient crops are needed [23,24] (Stockholm International Water Institute; http://www.siwi.org). To engineer stomatal responses and thus balance CO_2 intake and plant water loss, it is essential to understand the molecular mechanisms underlying guard-cell responses to water deficit (Box 2) [25]. ABA is a primary signal in response to drought. Upon water deficit, ABA is synthesized in roots and shoots [26,27] and is subsequently redistributed to the guard cells, where it triggers stomatal closure. This requires the coordinated control of several cellular processes, such as guard-cell turgor, cytoskeleton organization, membrane trafficking and gene expression [28,29]. ABA-deficiency (e.g. *aba3/los5* [30]) or insensitivity (e.g. *abi1* [31]) in vegetative tissues typically confers a wilting phenotype as a result of higher transpiration. Conversely, the *gcr1* mutant (G-protein-coupled receptor, GPCR1) is hypersensitive to ABA and has a drought resistance phenotype, as a result of lower rates of water loss [32]. However, under normal growth conditions it is

Box 2. ABA signaling in stomatal closure (Figure II)

Stomatal movement is a finely tuned response modulated by a complex network of control mechanisms, wherein abscisic acid (ABA) has a prominent role (see stomatal level subfigure; http://isotope.bti.cornell.edu/intro/intro_wue.html). Water shortage in the plant induces ABA accumulation, which in turn reduces stomatal conductance (g_s) and thus transpiration (E). Leaf water use efficiency (WUE) is expressed as the ratio of assimilation (A) and transpiration (E). However, caution is required because this parameter is not always correlated with crop WUE [24]. The stomatal perception of ABA leads to a multitude of responses, such as cytosolic pH increase, accumulation of reactive oxygen species (ROS), nitric oxide (NO) synthesis, ion channel activity modulation (both at the vacuolar and plasma membrane), increase in the concentration of cytosolic calcium ions, synthesis of lipid-derived second messengers and activation of protein kinases and phosphatases [64,65]. ABA is perceived by a yet unidentified ABA receptor (ABA-R) activating Ca^{2+} permeable channels (I). This activation is antagonized by both a protein phosphatase (PP) and the small G protein ROP10. ABA also activates Ca^{2+} channels via ROS and NO in a NAD(P)H-dependent manner (II). Mobilization of Ca^{2+} from internal stores is regulated by several players, such as cADPR (by activation of ADP ribosyl cyclase), Inositol-1,4,5- triphosphate (InsP3; derived from lipids through PLC activity) and Inositol hexakisphosphate (InsP6) (III). The ABA signal also triggers sphingosine kinase (SphK), which converts shingosine (SPH) in sphingosine-1-P (S1P). S1P induces stomatal closure in a process dependent on GPA1 (a Gα-subunit protein), whose function is inhibited by GPCR1, a G-protein-coupled receptor-like protein [32]. Most of these signals converge to affect Ca^{2+} level [66]. Whether $[Ca^{2+}]_{cyt}$ oscillations or calcium-independent pathways are implicated in stomatal response to ABA is still under debate [66,67]. ABA signaling downstream of Ca^{2+} is negatively regulated by the protein phosphatases ABI1 and ABI2. ABI2 associates with a calcineurin B-like protein (CBL1) and the CBL-interacting protein kinase 15 (CIPK15) to form a trimeric protein complex, and is inactivated by redox signals [64]. ABI1 is sequestered to the plasmamembrane by phosphatidic acid (PA; derived from ABA-activated PLD) [68]. This binding decreases ABI1 phosphatase activity and, consequently, promotes ABA response. The serine-threonine kinase OST1/SRK2E [43] functions downstream of ABI1 in the stomatal closure response [69,70] but upstream of cytoplasmic alkalinization [69]. ABA also induces the production of NO, which modulates ion channel activities and Ca^{2+} levels [67] (III).

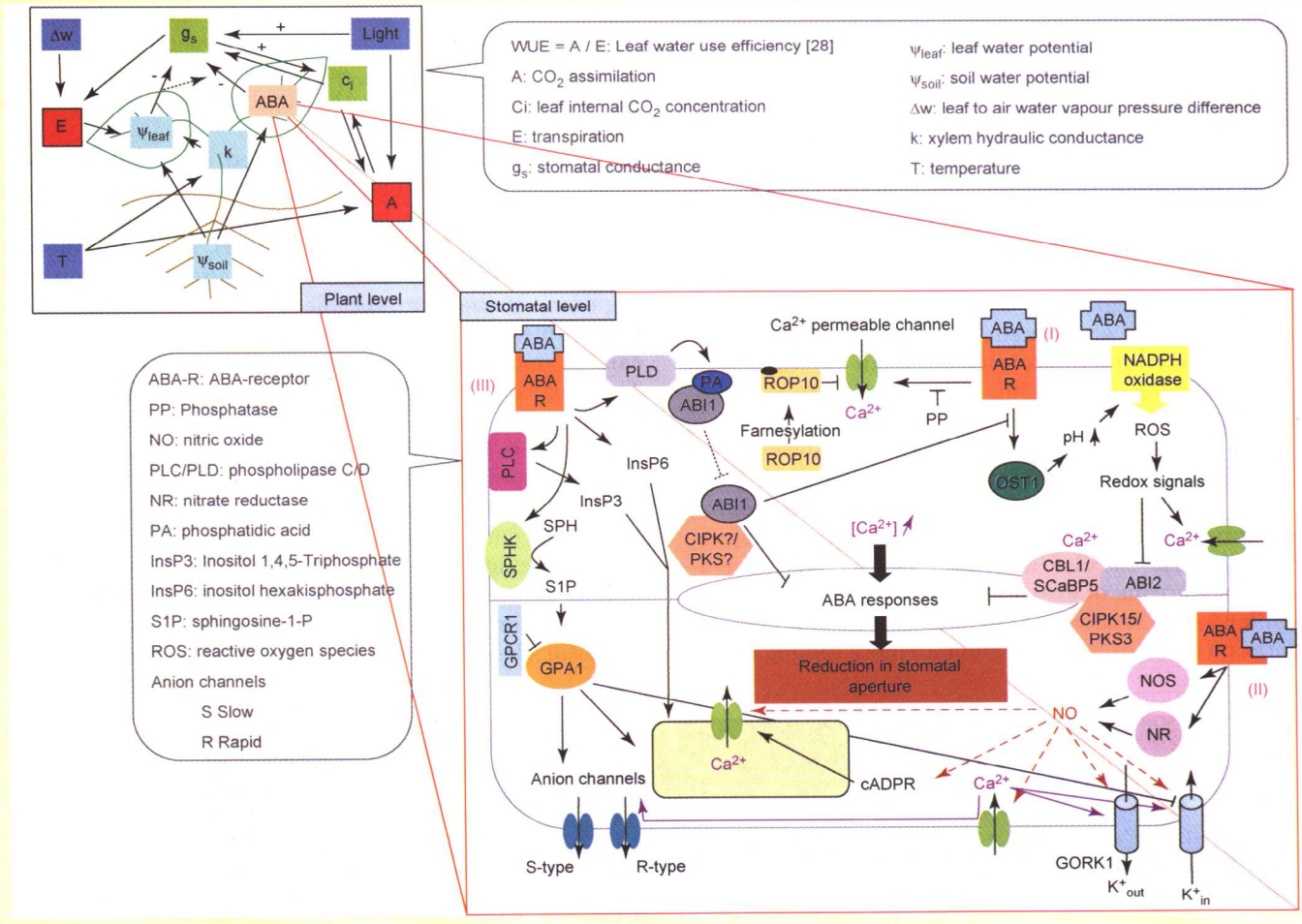

Figure II. ABA signaling in stomatal closure.

indiscernible from the wild type. This indicates that GPCR1 is a key factor in the regulation of stomatal closure and opening under drought stress.

The reduction in guard-cell turgor pressure that mediates stomatal closure involves the efflux of potassium and anions, and sucrose and malate removal [22,33]. A knockout mutant of the major voltage-gated potassium channel in the guard-cell membrane (guard cell outward rectifying K^+ channel, *gork1*) displays an increased level of transpiration (as expected from its inability to close its stomata) [22]. Importantly, this increased water loss is amplified under drought conditions, hinting at a

regulatory role of GORK1 in water retention. Furthermore, there is evidence that ABC-transporter proteins (multidrug resistance-associated proteins with an ATP binding cassette, MRP) are implicated in modulation of guard-cell ion-channel activities. Knockout mutants of *MRP4* and *MRP5* were assessed for effects on stomatal regulation [34,35]. Disruption of *MRP5* resulted in reduced opening of stomata in the light and, hence, reduced transpiration. In addition, stomatal closure in *mrp5* mutants was insensitive to ABA and Ca^{2+}. Importantly, *MRP5* deficiency also led to a higher leaf WUE compared to the wild type. By contrast, *MRP4* knockout mutants leave their stomata (that are sensitive to ABA) more opened both in light and darkness, and are less tolerant to dehydration. Likewise, the ABA-deficient *nced3* mutant, affected in a key-regulatory step in ABA synthesis [36], and *gork1* [22] displayed an increased water loss both in dark and light.

Although ABA is known to initiate the reactions of guard cells to drought (**Box 2**), it is likely that other signals can control stomatal movement independently of ABA. This is exemplified by the limited stomatal opening induced by light in the ABA-insensitive *mrp5* mutant. In addition, it was shown that stomatal closure can be induced by Cd^{2+} in the ABA insensitive mutant *abi1-1* [37].

Imaging techniques to quantify plant water usage

The basic question in monitoring stomatal responses to drought is: how can aberrant stomatal regulation in mutant plants be revealed efficiently? Modified water status can be highlighted by several methods: (i) visual or camera-based [38] assessment of wilting; (ii) recording weight loss (an integrative measurement of water loss over several hours) [8,32,36]; (iii) water uptake (potometric) measurements [34]; and (iv) monitoring of air humidity at the leaf level (porometry) [39]. However, all these procedures have the drawback of either having low precision, or being labor intensive and not fit for screening of an entire plant population [40]. Thermal imaging overcomes these hurdles and permits automated, non-invasive monitoring of evaporation at the leaf surface.

Similar to the function of sweat glands in animals, the evaporation of water from leaf stomata has a cooling effect. As a consequence of stomatal closure, transpiration (E) decreases, as does the associated heat loss, causing an increase in surface temperature. Thermography reveals the temperature distribution of objects by visualizing their emitted long-wave infrared radiation (i.e. thermal radiation typically near 10 μm) [41]. As water transport in plants is driven by leaf transpiration, thermal imaging can quantitatively estimate plant water usage. Under controlled environment conditions, VPD, air speed and light level are kept constant. Transpiration is then mainly determined by stomatal conductance because transpiration through the remaining part of the leaf surface (98.0–99.8%) represents only a fraction of the total transpiration (10–100 times lower) owing to the presence of a waxy cuticula [41]. However, leaf surface morphology (e.g. the absence of hairs) can alter the boundary layer conditions, which in turn influences leaf temperature. Stomatal conductance is the last step in the 'chain of events' controlling water use, but is influenced by the water availability within the plant (**Box 2**). Water uptake and transport also influence WUE; for instance, modified root architecture (e.g. more lateral roots [8]) could, in addition to an altered stomatal index and cuticular permeability, determine the final characteristics of the plant.

Thermography has been applied since the 1970s to detect disturbed plant water relations [42]. As an example, the progressive onset of drought stress can be visualized before visible wilting occurs (**Figure 1**). The use of thermal imaging to screen for mutants with altered transpiration is gaining momentum; specific responses to changes in key environmental factors, such as CO_2, humidity and light, can be monitored in real-time [31,43,44] (**Figure 2**). Thermography can also help to characterize transpiration kinetics in mutants isolated by alternative screening approaches. Thus, this technique provides new leads to the characterization of the signaling cascade for stomatal control. However, the implications of stomatal closure extend beyond the limitation of transpiration (E). Dependent on the light level and CO_2 availability, decreased CO_2 uptake can limit photosynthetic assimilation [45]. Thus, screening for water-conservation traits only (i.e. efficient stomatal closure), will probably be detrimental to crop

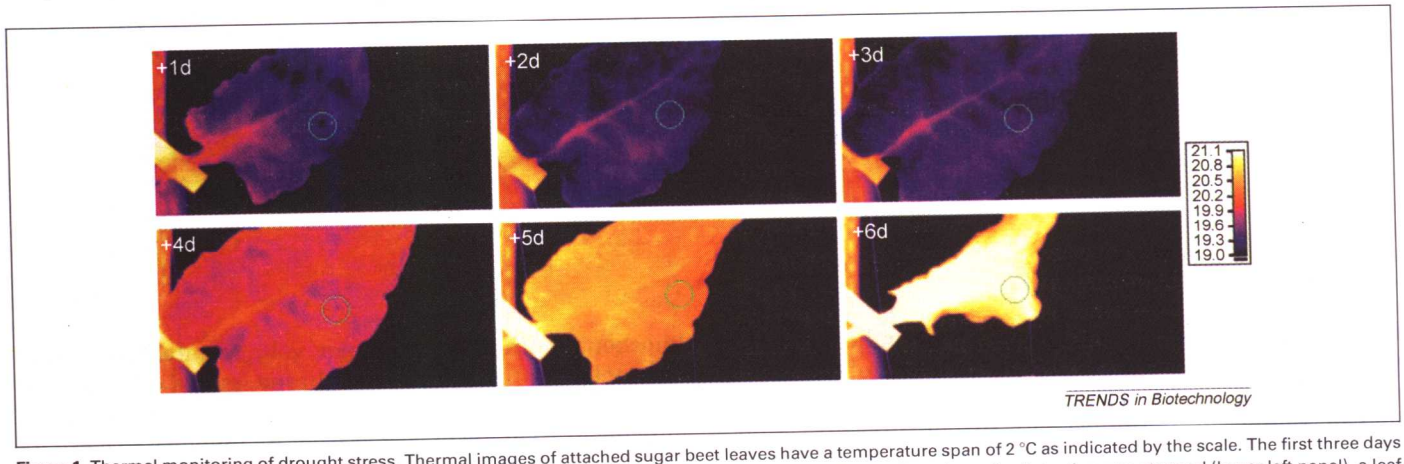

Figure 1. Thermal monitoring of drought stress. Thermal images of attached sugar beet leaves have a temperature span of 2 °C as indicated by the scale. The first three days after irrigation was stopped (upper panels), the leaf temperature in the indicated circular region was 19.2 °C. Four days after irrigation was stopped (lower left panel), a leaf temperature increase was apparent. Wilting occurred after six days (lower right panel) when the surface temperature had approached 20 °C.

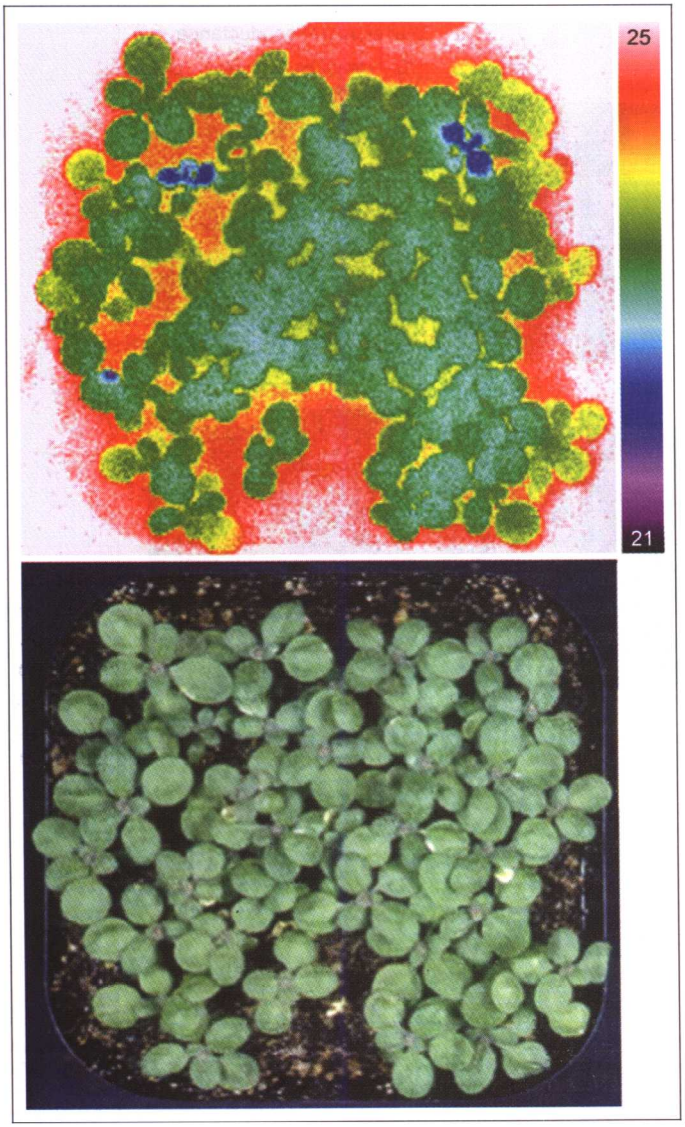

Figure 2. Mutant screening by thermal imaging. Highlighting *abi1–1* (abscisic acid insensitive) *Arabidopsis* mutants with a low leaf temperature phenotype within a population of wild-type plants. Top panel: thermal image. Lower panel: corresponding image in the visible spectrum.Temperature scale from 21 to 25 °C; mutants are more than 1 °C colder than the surrounding wild-type plants. Figure reproduced with permission from Ref. [31].

yield. Hence, additional monitoring tools are needed to ensure optimal photosynthetic yield.

Assessing photosynthetic yield

Assimilation can be quantified by measuring changes in CO_2 concentration at the level of leaves or plants enclosed in a cuvette [34]; however, this approach is not amenable to screening. Destructive determination of the carbon isotope signature of a plant at the end of the growth period (DELTA technique; http://www.csiro.au) yields an integrative account of assimilation efficiency [24], and is used to assess WUE. Using this approach, high yielding wheat cultivars were obtained. However, combined imaging of transpiration and assimilation would enable non-contact measurements throughout plant development.

Light absorbed by higher plants is only partially used for photo-assimilation. Dependent on temperature, light, CO_2 level and the photosynthetic capacity of plants, a variable share of the captured light energy is dissipated as heat (xanthophyll and/or lutein cycles) [46]. This thermal emission from leaves can be measured with a photoacoustic setup [47], which is non-imaging and requires the enclosure of the studied leaf-region in a gas-tight cuvette. In addition, a small fraction of the light quanta absorbed is re-emitted as chlorophyll fluorescence. This emission can be revealed after blue light excitation by imaging the emitted red fluorescence light [48], and has been used extensively to monitor a plethora of stress conditions [42]. The information derived from chlorophyll fluorescence emission at different light intensity levels (low non-photosynthetically active light, optimal light for photosynthesis and saturating light levels) gives an indication of the share of photochemical and non-photochemical 'quenching' (NPQ) processes [42,48]. From these measurements, parameters are derived that display a linear relationship with photosynthetic electron transport, thus reflecting carbon assimilation [49,50], which contributes to crop yield. As illustrated by **Figure 3**, local ABA-induced stomatal closure imposes a limitation on photosynthesis under high light conditions, which induces a concomitant increase in thermal dissipation (NPQ). Conversely, as expected from its higher stomatal density, the *sdd1* mutant (**Box 1**) displayed less NPQ in response to increasing light, compared with the wild type [51], which could be beneficial in field conditions. As a drawback, *sdd1* has a higher transpiration rate. By contrast, the *lsd*1 (lesion simulating disease) mutant shows a 50% reduction in transpiration and is unable to dissipate the excess excitation energy by NPQ, eventually leading to its runaway cell death (rcd) phenotype [39].

Finally, the response of plants targeted for field culture to combinations of stresses needs to be considered. More specifically, a thorough insight is needed into how plant stress-response networks interact [52]. Engineering drought resistance needs to be reconciled with optimal plant performance, which implicates fine-tuning of stomatal reactions under diverse environmental conditions, avoiding deleterious side-effects.

Towards screening for optimal WUE: perspectives for the future

Safeguards are required against relying solely on thermography to quantify stomatal conductance for screening purposes. Preferably, quantitative yield parameters should be followed up simultaneously. In this respect, a screening for alterations in chlorophyll fluorescence emission could help to highlight lowered photosynthetic efficiency. Based on the results of a first screening, candidate plants can be further submitted to short-term plant growth assays [42]. The combination of thermal and chlorophyll fluorescence imaging has been exploited previously to determine the quantitative link between stomatal conductance and chlorophyll fluorescence parameters as NPQ and photochemical yield of PSII [53]. To apply such screening strategy, cameras must be able to monitor populations of plants. Moving either plants ([54], http://www.lemnatec.com/scanalyzer_gh.htm, Traitmill) or camera systems [55] greatly expands the screening

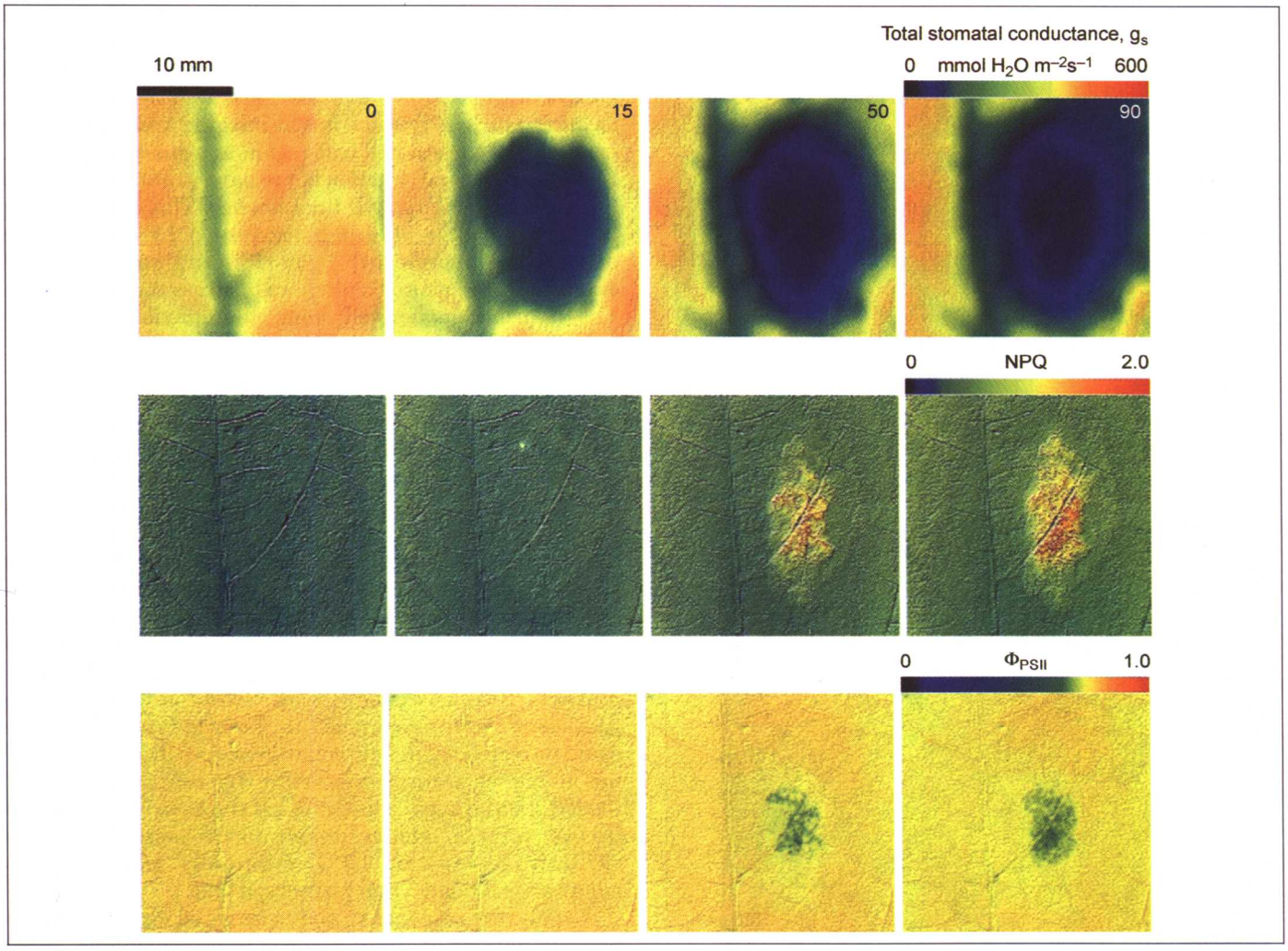

Figure 3. Combined thermal and chlorophyll fluorescence imaging. A kinetic analysis of stomatal conductance (gs) – as a measure of transpiration – and the chlorophyll fluorescence parameters, non-photochemical quenching (NPQ) and photochemical yield of photosystem II (Φ PSII) is shown. From left to right: just before abscisic acid (ABA) application, 15, 50 and 90 minutes after treatment. A decrease in gs and Φ PSII, and an increase in NPQ were visualized at the site of ABA treatment on an attached bean leaf. At lower illumination levels, no decrease in photochemical parameters is evident, while the response at higher light levels is exacerbated. Figure reproduced with permission from [53].

capacity of a setup. Quantification of performance is objectively assessed through image processing [38,56]. Such combined screening setups could be a 'test-bed' to assess the agricultural performance of engineered crops. Screening under stress-free conditions produces cultivars with superior performance also under mild drought stress, as exemplified by breeding in wheat [57]. Moreover, engineering drought resistance by inducible promoter constructs [25,46,58] will avoid the growth penalty associated with constitutive expression of the targeted genes. Plant engineering based on mutant analysis or, ultimately, on *in silico* testing of virtual plants [25,59] combined with crop simulation modeling [24], will be supported by the quantitative feedback from imaging-based assessment.

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