植物生态学报 2012, **36** (1): 88–98
Chinese Journal of Plant Ecology
doi: 10.3724/SP.J.1258.2012.00088
http://www.plant-ecology.com

干旱区叶片形态特征与植物响应和适应的关系

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摘 要 叶片形态是指示植物适应特定环境的重要指标。由于植物叶片形态不仅对时空环境变化具有极强的敏感性和可塑性, 而且能够通过叶片形态的调整调节自身的生存适应能力, 所以叶片形态学研究一直是植物生理及植物生态学研究中的热点。该文在总结前人叶片形态学研究成果的基础上, 探索建立了简单的叶片形态指标分类体系; 结合物质能量交换的物理学原理, 回顾总结了叶片表观形态变化与叶片物质能量交换之间的相关关系; 应用叶片形态影响物质能量交换的物理学原理, 重点分析了干旱区植物叶片表观形态对低水分环境、高辐射(或高温)的响应与适应特征; 最后, 在回顾分析的基础上, 对叶片形态研究中存在的几个问题进行了讨论。

关键词 干旱区植物, 叶片边界层阻力, 叶片形态学, 叶片温度, 植物响应与适应特征

A review of leaf morphology plasticity linked to plant response and adaptation characteristics in arid ecosystems

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Abstract

Leaf morphology is closely related to the specific environment and provides the most useful characteristics to understand plant response and adaptation strategy to environmental change. Leaf morphology plasticity is obviously related to the temporal and spatial variation of environmental variables, which are useful to plants to enhance their ability to survive. Consequently, for many years, studies on plant physiology, plant ecology and physiological ecology focused on leaf morphology. We establish a simple category of leaf morphology classification. Simultaneously, based on the principle of material and energy balances, we systematically review the relationships among environment, leaf morphology and energy balances (or material changes), and emphasize that leaf morphology responded or adapted to lower water availability and higher radiation (or temperature) in arid ecosystems. In conclusion, we submit and discuss existing problems in leaf morphology based on the weaknesses of previous studies.

Key words arid plant, leaf boundary layer resistance, leaf morphology, leaf temperature, plant response and adaptation characteristics

叶片形态是植物形态结构的重要组成部分, 并广泛应用于传统植物分类学(中国科学院中国植物志编辑委员会, 1998)。叶片形态不仅受基因控制, 同时对不同尺度环境变化都具有极强的敏感性(Nath *et al*., 2003; Hovenden & Vander Schoor, 2004; Tsukaya, 2005; López de Heredia *et al*., 2009; Picotte *et al*., 2009; 于贵瑞和王秋凤, 2010)。叶片形态对环境的响应和适应特征直接影响着植物与周围环境的物质和能量交换以及植物的生存能力和发展、变化方向(Smith & Geller, 1980; Nobel, 1991; Schuepp, 1993; Lambers *et al*., 2008; Vogel, 2009; 于贵瑞和王秋凤, 2010)。长期以来, 植物生理学家和植物生态学家对叶片形态保持着高度的关注, 并一直致力于发现并解释叶片形态变化的目的和意义(Ehlers, 1915; Pallas *et al*., 1967; Gates *et al*., 1968; Vogel, 1970; Morrow & Slatyer, 1971; Ehleringer *et al*., 1976; Smith & Nobel, 1977, 1978; Smith & Geller, 1980; Ehleringer, 1982; Geller & Smith, 1982; Nobel, 1991; Schuepp, 1993; Vogel, 2009)。同时, 我国研究者从叶片解剖结构(黄振英等, 1997; 何维明和张新

收稿日期Received: 2011-05-12 接受日期Accepted: 2011-10-31
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时, 2001; 邓艳等, 2004; 铁军等, 2008)、表观形态变化(徐文铎等, 2006; Xu *et al*., 2008, 2009)、生理性状特征(苏培玺等, 2003; 王俊峰和冯玉龙, 2004; 付爱红等, 2008; 薛伟等, 2011)等不同角度对叶片形态变化及其适应特征做了大量研究。但是, 以往大部分研究主要关注形态变化过程中叶片内部结构及生理性状的变化, 仅有少数研究涉及叶片形态与叶片表面物理过程的变化(傅伟和王天铎, 1994; 张良成和郭延平, 2001; 苏培玺等, 2003; 罗俊等, 2006; 李永华, 2010), 从而阻碍了我们对叶片形态变化与叶片内外物质、能量交换耦合关系的全面认识。为推动该领域的深入研究, 在前人研究基础上, 本文首先尝试对叶片形态指标进行分组; 其次, 从干旱地区植物对高温、低水分条件环境的生存适应能力出发, 利用基本的物理学原理, 着重解释了干旱区多年生植物叶片表观形态(或几何形态)变化的生理生态学意义; 最后, 在比较分析的基础上, 对叶片形态学现存的几个问题进行了分析探讨。

1 叶片形态指标分类

迄今为止, 研究者一直没有建立较为完整的叶片形态分类体系。为更好地开展叶片形态学研究, 本文根据前人研究中使用过的形态指标, 尝试将现有研究使用的叶片形态指标归为3类5组(表1)。

第一类为叶片解剖结构指标。叶片解剖结构是组成叶片形态结构的骨架, 并与植物自身保护, 叶片内外物质、能量交换具有直接的联系, 是研究叶片形态与植物生存适应特征的核心内容。该类指标的尺度十分微小, 主要通过显微镜观察记录(陆时万等, 1991; 潘瑞炽, 2004; Lambers *et al*., 2008; 李和平, 2009)。叶片解剖结构的研究历史较长, 涉及内容广泛而深入, 在此基础上已有研究者对其特征、功能做了详细的总结报道(周智彬和李培军, 2002; 李芳兰和包维楷, 2005)。为此, 本文不再将其作为重点讨论内容。

第二类为叶片表观形态指标, 我们将该类进一步分为3组, 包括非量化形态指标、可量化形态指标和平面几何形态指标(包括衍生几何形态指标)。描述性形态指标是人们对叶片形态最直观的初始认识, 多用于简单区分物种间的不同; 可量化形态指标能够进一步细化区分植物物种间的不同, 同时可用于量化研究植物生理过程变量及其变化特征(Ehleringer *et al*., 1976; Ehleringer & Mooney, 1978; Ehleringer, 1980; Geller & Smith, 1982; 陆时万等, 1991; Smith *et al*., 1997; 中国科学院中国植物志编辑委员会, 1998); 平面几何形态指标(包括衍生几何形态指标)用于描述叶片平面几何特征, 从而为定量、精确地确定不同物种间的差异特征提供重要的可比参数(Parkhurst & Loucks, 1972, 陆时万等, 1991; 中国科学院中国植物志编辑委员会, 1998), 同时随着计算机图形学的发展以及叶片形态变化与植物生理过程关系研究的深入, 可量化形态指标与平面几何形态指标能够进一步为叶片生理过程机理模型提供参数(Nobel, 1991; 于贵瑞和王秋凤, 2010)。从现有研究分析, 该类指标既是人们认识叶片特征的出发点, 也是现阶段叶片形态研究中的重点和薄弱环节。

第三类为与叶片形态密切相关的叶性状指标(如比叶面积和叶片氮含量等), 由于该类指标与植物生理过程密切相关, 所以在近20年的相关研究中一直备受关注(Field & Mooney, 1986; Wright *et al*., 2001, 2004; 张林和罗天祥, 2004)。叶片形态与叶性状指标相关关系的研究, 有利于我们更为全面地认识叶片形态变化的生理生态学意义。

在有关叶片形态的研究中, 由于前人对于叶片解剖结构、叶性状(如叶寿命、比叶面积、叶氮含量等因子)的研究现状及未来发展已有了较为全面的回顾总结(周智彬和李培军, 2002; 张林和罗天祥, 2004; 李芳兰和包维楷, 2005; 孟婷婷等, 2007), 所以本文对叶片解剖结构及叶性状指标的内容不再展开讨论, 而重点关注叶片表观形态(或几何形态)的变化及对叶片物质、能量交换的影响。

2 形态对叶片物质能量交换过程影响的物理学原理

2.1 形态对叶片水分、CO_2交换影响的原理

根据菲克定律(Fick's Law), 叶片与外界物质交换与叶片内外物质浓度差及扩散阻力直接相关(公式(1))。

$$J = \Delta C/r \quad (1)$$

J为单位时间单位面积的物质交换量, ΔC为叶片内外物质浓度差, r为叶片阻力。叶片阻力包括叶片内部阻力和叶片边界层阻力。叶片内部阻力指示了物质从叶片内部扩散到叶片表面的阻力, 包括了

doi: 10.3724/SP.J.1258.2012.00088

表1 叶片形态指标分类
Table 1 Classification of leaf morphology index

分类(组) Classification (group)	参数 Parameter	功能和用途的简要描述 Brief description of function or application
类1: 叶解剖结构指标 Class 1: Leaf anatomical classification	角质层厚度 Cuticle thickness	影响叶片内外物质、能量交换, 保护叶片 Relating to leaf material and energy exchange, and leaf defense
	栅栏组织厚度 Palisade tissue thickness	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	海绵组织厚度 Spongy tissue thickness	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	叶片厚度 Leaf thickness	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	气孔密度 Stomatal frequency	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	气孔开度 Stomatal aperture	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	气孔下陷深度 Stomatal pore depth	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	海绵组织细胞间隙 Intercellular space	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
类2 (组1): 非量化形态指标 Class 2 (group 1): Non-quantifiable classification of leaf morphology	如针叶、阔叶 E.g. coniferous and broad-leaved	应用于植物分类学 Relating to plant indentification
	如披针形叶、卵形叶 E.g. lanceolate leaf shape and ovate leaf shape	应用于植物分类学 Relating to plant indentification
类2 (组2): 可量化形态指标 Class 2 (group 2): Quantifiable classification of leaf morphology	叶脉 Leaf vein	影响叶片水分传输，应用于植物分类学 Relating to water transport and plant indentification
	叶柄 Leaf-petiole	影响叶片水分传输和光合生理，应用于植物分类学 Relating to water transport，photosynthetic physiology and plant indentification
	托叶 Stipule	应用于植物分类学 Relating to plant indentification
	表面绒毛 Leaf hair	影响叶片内外物质、能量交换, 应用于植物分类学 Relating to leaf material and energy exchange, and plant indentification
	叶角 Leaf orientation	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
类2 (组3): 平面几何形态指标及其衍生指标 Class 2 (group 3): Geometry and derivative geometry classification of leaf morphology	叶长 Leaf length	应用于植物分类学 Relating to plant indentification
	叶宽 Leaf width	应用于植物分类学 Relating to plant indentification
	叶周长 Leaf perimeter	无明确生理生态学意义 No clear ecophysiology significance
	叶面积 Leaf area	影响叶片内外物质、能量交换 Relating to leaf material and energy exchange
	叶齿 Leaf teeth	影响叶片内外物质、能量交换, 应用于植物分类学 Relating to leaf material and energy exchange, and plant indentification
	裂叶 Leaf lobe	影响叶片内外物质、能量交换, 应用于植物分类学 Relating to leaf material and energy exchange, and plant indentification
	叶长/宽比 Ratio of leaf length to width	无明确生理生态学意义 No clear ecophysiology significance
	面积/周长比 Ratio of leaf area to perimeter	无明确生理生态学意义 No clear ecophysiology significance
类3: 与叶片形态密切相关的其他指标 Class 3: Other classification closely related to leaf morphology	比叶面积 Specific leaf area	影响叶片投资收益率 Relating to leaf benefit-cost ratio
	叶片氮含量 Leaf nitrogen content	影响叶片光合生理与水分利用效率 Relating to leaf photosynthetic physiology and water use efficiency
	叶寿命 Leaf lifespan	影响叶片投资收益率 Relating to leaf benefit-cost ratio
	叶片含水量 Leaf water content	影响叶片表面能量平衡及干物质含量 Relating to leaf energy balances and dry matter content
	光吸收比例 Light-absorption rate	影响叶片表面能量平衡 Relating to leaf energy balances

叶肉组织阻力、细胞间隙阻力、角质层阻力和气孔腔阻力。实际计算中考虑到角质层阻力和叶肉组织阻力十分微小, 常将其忽略, 并仅用细胞间隙阻力与气孔腔阻力来计算叶片内部阻力(称为气孔阻力, r_{st})。这样, 叶片内部物质扩散到叶外的阻力可以通过r_{st}与r_b (叶片边界层阻力)计算, 所以叶片与外界物质交换方程变换为公式(2) (于贵瑞和王秋凤, 2010):

$$J = \Delta C / (r_{st} + r_b) \quad (2)$$

实际测定中, 气孔阻力可用气孔计测定(计算)。但是, 叶片边界层阻力获得较为困难, 现在常用模拟叶片结合热平衡法测定或通过计算机仿真模拟获得(Roth-Nebelsick, 2001; 张良成和郭延平, 2001)。然而, 由于真实叶片变化复杂, 且真实叶片与模拟叶片差别较大, 所以很难通过大量模拟获得每片叶子的边界层阻力。为简化叶片边界层阻力的模拟测定, 研究者常通过叶片边界层厚度与物质扩散系数计算获得叶片边界层阻力(公式(3)) (Nobel, 1991):

$$r_b = \delta_b / D_j \quad (3)$$

式中, D_j为物质扩散系数(不同物质在不同温度下扩散系数不同, 可以通过扩散系数表查找获得, 如20 ℃环境下水蒸气在空气中的扩散系数为$2.42 \times 10^{-5} \cdot m^3 \cdot s^{-1}$)。$\delta_b$为叶片边界层厚度。计算过程中, 边界层厚度可用经验公式(公式(4))获得(Nobel, 1991):

$$\delta_b = A\sqrt{l/v} \quad (4)$$

式中, δ_b的单位为mm, l为沿风向流动方向的叶片平均长度(或叶片特征尺寸, 实际应用中常用叶片最大宽度替代), 单位为m, v为环境风速,单位为$m \cdot s^{-1}$, A为经验常量, 在气温20–25 ℃环境下A等于4.0, 同时气温每增加10 ℃, A增加幅度约为3%。

2.2 形态对叶片表面能量交换影响的原理

根据叶片能量守恒定律, 叶片表面能量变化(S)决定于吸收(S_{in})和逃逸(S_{out})叶片表面的能量差值。到达叶片表面的能量包括叶片吸收的直接辐射和叶片从周围环境吸收的散射辐射。如果叶片距离地面较远, 那么叶片从周围环境吸收的散射将主要包括天空和云的散射辐射。气象学上将太阳直接辐射, 天空和云散射辐射的总量称为总辐射(S_s), 并且可以通过总辐射仪测定(Nobel, 1991; 周淑贞, 1997)。如果定义α为叶片对辐射的吸收率, 那么叶片吸收的辐射能量可表达为公式(5)。

$$S_{in} = \alpha S_s \quad (5)$$

逃逸叶片表面的能量包括叶片红外辐射、热对流、热传导、热湍流和表面水汽蒸发。根据斯蒂芬-波尔兹曼定律(Stefan-Boltzmann Law), 叶片红外辐射(J_I)可表达为公式(6) (Nobel, 1991; 周淑贞, 1997)。

$$J_I = \alpha_{leaf}\, \sigma T^4 \quad (6)$$

式中, α_{leaf}为相对辐射率, 表示叶片辐射能力与同一温度下黑体辐射能力的比值; σ为斯蒂芬-波尔兹曼常数, 等于$5.67 \times 10^{-8}\ W \cdot m^{-2} \cdot K^{-4}$; T为绝对温度。

根据菲克定律, 通过热对流、热传导、热湍流带走的能量(J_V)可表达为公式(7) (Nobel, 1991)。

$$J_V = \frac{T_{leaf} - T_{air}}{r_b} = D_j \frac{T_{leaf} - T_{air}}{\delta_b} \quad (7)$$

式中, T_{leaf}为叶片表面温度, T_{air}为空气温度。

如果用V_h表示单位时间单位面积叶片水分蒸腾量, 用E_{vap}表示单位水分体积蒸发所需的能量(E_{vap}与温度直接相关, 25 ℃环境下E_{vap}= 44 $kJ \cdot mol^{-1}$), 那么叶片表面水汽蒸发带走的能量(J_H)可用公式(8)表示为:

$$J_H = V_h E_{vap} \quad (8)$$

综合公式(5)–(8), 单位面积上叶片能量平衡可表达为公式(9)。

$$S = S_{in} - S_{out} = \alpha S_s - \alpha_{leaf}\, \sigma T^4 - D_j \frac{T_{leaf} - T_{air}}{\delta_b} - V_h E_{vap} \quad (9)$$

3 旱区植物叶片形态变化的生理生态学意义

依据叶片形态在叶片物质能量交换过程中的物理学原理, 本节将重点讨论干旱区多年生植物在高辐射、高温和低水分环境下, 叶片形态的响应及适应特征。同时, 根据未来干旱地区气候变化预测, 讨论叶片形态变化对降水变化的响应与适应特征。

3.1 干旱区植物叶片形态变化与高温限制

温度对所有生物生理活动具有调节作用。通常, 只有保持在某个合理的温度区间, 生物有机体才能保证生理活动的正常运行, 高于或低于这个温度区间都将对生物的生存发展带来不利影响(潘瑞炽,

doi: 10.3724/SP.J.1258.2012.00088

2004; Lambers *et al*., 2008)。从而温度成为生物学研究中揭示生物物质能量存储、交换过程的主要因子。

在干旱地区, 高温限制是影响生长季节叶片光合作用、呼吸作用及水分和养分利用的直接因子(Osmond *et al*., 1987; Schulze *et al*., 1987; Lambers *et al*., 2008)。据2010年我们观测的气象数据, 我国民勤、磴口、敦煌最高气温均超过40 ℃ (未公开数据)。在生长季节晴朗的天气条件下, 干旱区植物叶片温度往往高于气温。据相关研究报道, 当空气温度达到30 ℃时, 荒漠地区植物叶片温度能够达到40–50 ℃, 这一温度已触及植物叶片能够承受的极限(Smith & Nobel, 1977; Smith, 1978; Osmond *et al*., 1987; Knight & Ackerly, 2003; Nicotra *et al*., 2008)。所以, 在极端高温环境下, 能否成功地降低叶片温度成为干旱地区植物生存的关键。

根据公式(9)可知, 控制植物叶片温度升高的方式可以通过节源(降低叶片吸收辐射比例)和开流(增加热对流、热传导、热湍流散热和水分蒸腾散热)实现。研究显示, 随着辐射的增加, 植物叶角、单位叶片面积上的叶片表面绒毛均出现增加趋势(Ehleringer *et al*., 1976; Ehleringer & Mooney, 1978; Medina *et al*., 1978; Ehleringer, 1980; Smith *et al*., 1997; Schrader *et al*., 2004; Picotte *et al*., 2009)。植物叶角增加可以直接降低叶片对辐射的吸收比例, 而叶片绒毛的增加能够增强叶片对辐射的反射比例(Ehleringer *et al*., 1976; Ehleringer & Mooney, 1978; Medina *et al*., 1978; Ehleringer, 1980; Smith *et al*., 1997; Picotte *et al*., 2007)。

水分蒸腾是降低植物叶片温度的重要方式(Lambers *et al*., 2008)。然而从清晨到中午, 随着时间的推移和植物体内水分的快速损失, 干旱区植物叶片水势往往具有降低的趋势(李向义等, 2004; 宋耀选等, 2005; 付爱红等, 2008), 即在高温限制逐步增强的过程中蒸腾降温逐步减弱, 而这一过程对干旱地区植物存活极为不利。为此, 在干旱、高辐射环境下, 植物将倾向于选择增加热对流、热传导、热湍流来增加叶片散热(公式(7)), 即通过叶片几何形态变化(如降低叶片尺寸(宽度)、增加裂叶或叶齿面积和深度)降低边界层阻力(Bragg & Westoby, 2002; McDonald *et al*., 2003; Thuiller *et al*., 2004; Rozendaal *et al*., 2006; Picotte *et al*., 2007, 2009; Yates *et al*., 2010)。需要强调的是, 在风速较低, 叶片水势下降迅速, 气孔开度降低或关闭的情况下, 通过降低边界层阻力(改变叶片形态)降低叶温的方式对植物躲避高温伤害尤为重要(Vogel, 2009; Yates *et al*., 2010)。

3.2 干旱区植物叶片形态与水分因子

水分是控制干旱地区植物存活发展的关键限定因子(Noy-Meir, 1973)。干旱地区物种(除一年生短命草本植物)为增加自身的生存适应能力, 一方面要尽可能地减少水分损失, 另一方面要极力提高水分利用效率。干旱地区植物减少水分损失往往是通过降低叶面积指数、单叶面积等来实现(McDonald *et al*., 2003; Rozendaal *et al*., 2006; Picotte *et al*., 2007; Lambers *et al*., 2008; 黄玫和季劲钧, 2010)。提高水分利用效率涉及叶片形态及叶片性状的多种变化。例如, 利用增加叶片表面绒毛等方式增加反射率, 从而降低叶温, 促进光合反应速率(Smith & Nobel, 1977; Ehleringer & Mooney, 1978; Ehleringer, 1980, 1982); 在单叶面积降低的同时往往伴随着叶片厚度、单位面积叶片重量和叶氮含量的增加(Abrams *et al*., 1994; Wright *et al*., 2001; Rozendaal *et al*., 2006), 由于叶片厚度和单位面积叶重量与叶片内外面积比、叶片内含物(如水分、大分子物质等)存在明显的正相关关系, 所以厚度和单位面积叶重量增加不仅可以增加叶片保水性, 而且可以减缓叶温升高的速率, 而叶氮含量的增加能够提高叶片的光合速率, 从而提高植物对有限水分的利用效率(Smith & Nobel, 1977; Field *et al*., 1983; Field & Mooney, 1986; Knight & Ackerly, 2003)。

干旱地区降水最为显著的特征表现为降水稀少, 年际及季节变化幅度巨大(陈佐忠和汪诗平, 2000)。这一背景植物叶片形态结构如何调整才能更好地适应水分动态的变化?相关研究结果显示, 植物在干旱年份叶片面积变小过程中, 叶片宽度具有优先降低的趋势; 而植物在湿润年份叶片面积变大的过程中, 叶片长度显现优先增长的特征(Balota *et al*., 2008; Picotte et *al*., 2009; 李永华, 2010)。

从数学角度考虑, 叶片长短轴(常表述为叶片长和宽)变化具有以下特征, 短轴优先变化利于叶面积快速变化, 而长轴优先变化有利于叶片周长的变化, 同时阻止叶面积的快速变化。根据**3.1**的分析, 我们很容易认识到, 干旱年份在水分压力明显增强

的同时, 植物将面临更高的辐射及温度压力, 叶片宽度的优先降低一方面可以快速降低叶面积, 从而降低植物总体水分损失量, 另一方面将促使叶片阻力的快速降低, 从而增强植物叶片在低蒸腾水平下的降温能力。在湿润年份, 水分胁迫得以部分缓解, 使植物叶片长度优先增加, 一方面可以阻止由于叶面积快速增加带来的植物体水分大量损失, 另一方面能够在适当增加叶片光合面积的同时使叶片边界层阻力维持在较低的水平, 从而抵御高温的伤害。

4 叶片形态研究中的几个问题

4.1 应用叶片形态指标计算叶片边界层阻力

裂叶或叶齿是干旱区植物叶片较为普遍的表观特征。裂叶或叶齿不仅对环境变化具有较高的敏感性, 同时也直接影响植物适应干旱、高辐射环境的能力(Sisó *et al*., 2001; Nicotra *et al*., 2008; Royer *et al*., 2009)。虽然研究者认同叶片裂叶或叶齿变化与叶片边界层阻力有关, 但遗憾的是, 我们现有对叶片边界层阻力的认识仍维系于叶片宽度(以叶片宽度作为叶片特征长度), 无法直接证明裂叶或叶齿变化与叶片边界层阻力之间具有直接的相关关系, 从而无法深入解释裂叶或叶齿变化对叶片物质、能量交换的影响(Smith & Geller, 1980; Nobel, 1991; Schuepp, 1993; Sisó *et al*., 2001; Nicotra *et al*., 2008; Royer *et al*., 2009)。而解决这一问题的关键在于深入理解叶片边界层阻力的物理意义, 寻找更为合适的叶片形态学指标(或叶片特征长度), 通过对叶片形态指标与叶片边界层阻力相关关系的深入分析, 建立更为完善的叶片边界层阻力模型。

通过公式(3)和(4), 我们发现边界层厚度是联系叶片形态与叶片边界层阻力的直接桥梁。Schuepp (1993)认为叶片边界层平均厚度的物理意义应该根据叶片内部距离叶片边缘的权重平均距离进行定义。换句话说, 叶片某点的边界层厚度是由该点与叶片边缘的最近距离直接控制。研究者利用人工模型模拟、计算机仿真模拟以及热感相机测定技术证实, 不同形态叶片, 表面某点的流热传导速率随该点距离叶片边缘的距离增加而增加(Vogel, 1970; Roth-Nebelsick, 2001; Stokes *et al*., 2006; Vogel, 2009)。事实上, 虽然研究证明Schuepp (1993)关于叶片边界层平均厚度的定义是正确的, 但实际应用中我们仍很难应用数学积分和统计的方法对大量叶片求算其边界层厚度。然而, 如果换个角度分析, 首先对叶片进行网格化处理, 就可以清晰地认识到: 叶片边界层平均厚度(或阻力)应该与单位边距长度(周长)所包围的叶片面积(网格单元数目)直接相关(Roth-Nebelsick, 2001)。由于利用现代图像分析技术我们很容易获得叶片的周长和面积, 所以应用面积/周长比作为叶片的特征长度估算叶片边界层平均厚度(或边界层阻力)不仅具有可靠的理论依据, 而且在处理复杂叶片形态时具有巨大的实践价值。

4.2 叶片边界层阻力与气孔阻力的关系

叶片边界层阻力和气孔阻力是控制叶片内外物质交换的关键环节。我们注意到, 随着水分有效性的降低、单叶面积(宽度)的减小, 叶片边界层阻力具有降低的趋势(公式(4)), 即随着叶面积(宽度)的减小, 叶片水汽蒸腾速率有可能增加, 从而降低叶片水分利用效率。事实上, 干旱地区植物叶片水分蒸腾变化十分复杂。在不同温度、气孔阻力下, 随着叶片尺寸(宽度)的减小(或边界层阻力的降低), 叶片蒸腾速率可能出现或增加或降低或不变的复杂格局(Smith & Geller, 1980)。与此对应, 来自于叶片δ^{13}C测定数据显示, 在降水量小于300 mm的干旱地区, 随着降水量的进一步减小, 植物叶片水分利用效率也出现或增加或降低或不变的复杂格局(Schulze *et al*., 1998, 2006; 苏波等, 2000; 王国安和韩家懋, 2001)。

为进一步解释叶片内外CO_2、水分交换及叶片水分利用效率变化机理(公式(2)), 我们既要关注气孔变化对水、CO_2交换影响的差异性, 又要深入理解边界层阻力与气孔阻力的共变规律(Jarvis & McNaughton, 1986; Wullschleger *et al*., 1998; Lambers *et al*., 2008)。

从现有研究水平看, 几乎没有直接的研究或数据说明二者共变过程或规律。间接的研究结果表明, 叶片边界层阻力降低(叶片变小或变窄)过程能够加速叶片蒸腾(公式(1)–(4)); 随着叶片植物水分的快速流失, 叶片水势降低, 叶片气孔开度会逐步降低, 甚至关闭(Tardieu & Simonneau, 1998; Lambers *et al*., 2008; 于贵瑞和王秋凤, 2010)。即叶片边界层阻力与气孔阻力具有负相关关系。如果这一关系得以证实, 并进一步获得气孔阻力随边

doi: 10.3724/SP.J.1258.2012.00088

界层阻力变化的幅度，那么我们能够更好地理解干旱地区不同物种在未来环境变化过程中的生存能力及适应特征。

4.3 叶片形态在植物生理生态学模型中的应用

叶片形态的模拟是进一步将叶片形态引入植物生长动态模型或区域植被动态模型的基础。现阶段，研究者已能够通过对叶片形态的数学分析建立静态的叶片形态模型(胡少军等，2007；吴谦等，2008)。然而，由于缺乏对叶片形态随环境变化机理及形态变化与植物生理生态过程内部耦合关系的清晰认识，所以无法模拟“环境-叶片形态-叶片生理生态学过程”。从现有研究基础看，我们迫切需要寻找既能指示植物生理生态学变化过程又能综合反映叶片形态特征的关键形态指标(例如面积/周长比，叶面积)，同时通过叶片关键形态指标与环境因子关系的研究，依据叶片物质能量交换的基础物理模型(参见**2.1**、**2.2**部分)，建立综合的“环境-叶片形态-叶片生理生态学过程”机理模型。

未来气候变化对植被动态的影响是现有干旱生态系统研究中的热点之一。建立在已有观测数据和相关假设的基础上，有研究预测未来我国干旱荒漠地区降水量将出现不同程度的增加(Gao *et al*., 2001；施雅风等, 2002, 2003；王英等, 2006; Parry *et al*., 2007；徐利岗等, 2009)。在这一背景下，利用“环境-叶片形态-叶片生理生态学过程”动态机理模型，从植物对环境变化响应最为敏感的叶片角度进行研究，将为更好地揭示干旱区植物物种生存、演化及区域群落结构、动态，为未来荒漠地区植被保护与恢复提供科学依据。

致谢 中央级公益性科研院所基本科研业务费专项(CAFYBB2007008)、林业公益性行业科研专项经费(201104077)和国家自然科学基金(40971283)资助。

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