

果树树形的形成机制与调控技术研究进展

张抗萍^{1a}, 李荣飞^{1a}, 常耀栋¹, 梁国鲁¹, 陆智明¹,
易佑文², 胡涛³, 鲁振华⁴, 郭启高^{1*}

(¹西南大学园艺园林学院, 重庆北碚 400715; ²广安市科技开发培训中心, 四川广安 638500;
³广安区农业局, 四川广安 638500; ⁴中国农业科学院郑州果树研究所, 郑州 450009)

摘要: 树形培养与维护是形成理想树体结构的基础。不同果树种类或同一种类在不同栽培条件下的适宜树形有所差异, 筛选与应用具有通风透光、高光能利用率、低成本、丰产、稳产、优质等特点的适宜树形是大多数果树生产者的共同目标。果树树形含自然树形和人工培育树形, 众多研究者通过不同树形结构特点及其修剪效应的对比分析, 逐步完善果树树形培养与维护的技术体系, 并提出冠层分枝与节间长度遗传特点、激素与矮化基因调控树形的机制。为此, 本文对果树的树形类型、形成调控机制、人工整形修剪技术, 以及树形的培养与维护等方面的研究现状进行了综述, 并对省力化机械修剪、树形形成调控机制及适宜树形的合理评价方法等进行了展望, 以期对果树树形培养和科学修剪提供参考。

关键词: 果树; 树冠结构; 形成机制; 整形修剪; 调控技术

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A review of the canopy architecture formation mechanism and regulation technology in fruit trees

ZHANG Kangping^{1a}, LI Rongfei^{1a}, CHANG Yaodong¹, LIANG Guolu¹, LU Zhiming¹, YI Youwen², HU Tao³, LU Zhenhua⁴, GUO Qigao^{1*}

(¹College of Horticulture and Landscape Architecture, Southwest University, Beibei 400715, Chongqing, China; ²Guang'an Science and Technology Development and Training Center, Guang'an 638500, Sichuan, China; ³Guang'an District Agricultural Bureau, Guang'an 638500, Sichuan, China; ⁴Zhengzhou Fruit Research Institute, CAAS, Zhengzhou 450009, Henan, China)

Abstract: Understanding the fundamental nature of an ideotype tree's structural characteristics is often a catalyst for the development of new technologies in fruit cultivation and management. It is widely believed, as demonstrated in the overwhelming majority of fruit tree species, or the same species cultivated in different natural conditions, that a tree's structural characteristics such as a training system, branch type, canopy position and crop load affect the yield and quality of the fruit. Indeed, studies have uncovered multiple overlapping but functionally distinct optimum canopies in fruit trees, including the natural canopy (no pruning) and different types of training systems (Spindle shape, Open center shape, Y-shape, T-shape, V-shape, etc.). The characteristics of different training systems and canopy structures of fruit trees can be evaluated by using morphological, cytological, physiological, biochemical and molecular measurements. There are many parameters that can be measured in fruit trees that have been associated with a tree structure. The different parameters reported among the training systems tested could be associated with the different capabilities of each system to intercept and distribute the light in the canopy. So natural light availability within fruit trees is an important factor for canopy and fruit development as light radiation provides energy for photosynthetic organisms and to motivate photosynthetic processes. Actually,

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作者简介: 张抗萍, 女, 在读博士研究生, 研究方向为果树树形培养。Tel: 18584564192, E-mail: 1164613516@qq.com。a为共同第一作者。

*通信作者 Author for correspondence. Tel: 023-68250383, E-mail: qgguo@126.com

when considering the single tree canopy for a given genotype, highly vigorous growth of a canopy gradually reduces the light penetration from top to bottom of the canopy. That is, the top/outer portions of a canopy intercept more light than the inner/bottom portions, and the photosynthetically active radiation (PAR) transmitted portion gradually decreases when light passes through a fruit tree canopy, which generates the light's microclimate and determines the amount of available light for distribution location within the canopy. Furthermore, the capability of light transmitting through a canopy intercepted by the inner/bottom portions is affected by many factors such as cultivation spacing, canopy architecture and fruit tree management practices including pruning, thinning and laying mulch using reflected light, etc. Consequently, the selection and application optimum training system is important, which is benefited by creating a better light microclimate and providing guidance for fruit manipulations, especially for the practicing of high and stable yields, high quality and lower cost production. And this has long been a focus for researchers in the past few decades. In this paper, we will first review the different training systems, there are more than 20 types of training systems applied in 13 genus listed in the table, which is just a part of the various applications in fruit trees, but are the most commonly used and some improved training systems have also been listed, such as round shape, spindle shape, improved spindle shape, open center shape, Y-shape, T-shape, V-shape, Columnar shape and so on. Through the comparative experiments of different training systems, researchers specifically selected some of the optimum training systems for different species cultivated in different natural conditions. This paper will bring forward a second point, that is, the mechanism of formation and regulation for training systems. We will show that the results of the mechanism, including the characteristics of branching and internode length genetics, dwarf gene expression and regulation, hormone content and their proportion are involved. The researches about the dwarf and semi-dwarfism regulation gene successfully cloned in peach, apple and pear etc, provide a direct and efficient approach for new cultivar breeding and the study of special gene sites. Especially, semi-dwarfism on root stock can provide a long-distance transport of mRNA from grafts and reduce the stature of a scion, in which the result presented clearly indicates that it would be applicable for regulating the fruit tree canopy. Though there is not a full understanding about the network for tree structure genes' regulation pathway, it points to further opportunities for studying the tree structure formation mechanism from the perspectives of related genes. Over recent decades, researches have been conducted in obtaining and keeping optimum tree structures to investigate the effects of pruning (including pruning period and method) on tree canopy growth, light microclimate, fruit yield and quality etc. The researchers stated that many growth and development characteristics such as photosynthetic efficiency, flower bud formation, fruit set, color, size, soluble solids and fruit maturity and so on are influenced by pruning. Moreover, some of the researchers studied the effect of a combination of the training system and rootstock (including root system) on light microclimate, fruit yield and quality. All of the research about relationships between orchard training systems and fruit yield and quality would assist in optimizing tree canopy pruning strategies. In this article we aim to provide an overview of canopy structural characteristics in fruit trees, summarize the mechanism of formation and regulation for training systems, review the current progress in pruning technologies and correlation, and prospect the potential applications of mechanical pruning, molecular mechanism of tree structural formation and regulation, and provide a reasonable evaluation method for different training systems. Furthermore, the limitation that should continue to make research on these topics are proposed, which will provide a beneficial reference for fruit tree manipulations.

Key words: Fruit tree; Canopy architecture; Formation mechanism; Pruning; Regulation technology

果树树形的形成受诸多因素的共同调节,如基因遗传调控、人工整形修剪以及立地环境的影响等。每种树形均有其独特的冠层微环境,影响树体对光、水、肥的利用,造成冠层不同部位的叶片营养与果实产量和品质的差异^[1-7]。若任果树干、枝、叶的自然特性生长,很难实现丰产、优质、安全的生产目标。果树冠层郁闭、树形管理成本高是果树栽培现行的普遍问题^[8-9]。在丰富的果树种质资源、广泛的分布范围和复杂的气候条件下,针对不同果树种类进行合理整形修剪,是建立与完善果树树形及其评价体系的现实需求,对果树栽培有重要的实践指导意义。由此,人们对不同树形的适用性进行了大量的研究。研究发现,适宜的树形可提高冠层的透光性^[7]、再成花率^[10]、结果枝的比例,利于碳水化合物分配,平衡营养生长与生殖生长,实现树体的连续结果^[11-14]。此外,整形修剪可提高树体的抗性^[15-16]和果实品质^[17]。近年来,运用分子生物学手段从育种层面筛选树形调控基因,也已成为当前研究的热点。为此,笔者在综述国内外果树树形演变与发展的基础上,总结了不同种属果树树形类型,以及树形形成机制及调控技术,以期为不同果树的树形选择、生理生态效应及推广等相关研究提供参考。

1 果树树形类型

根据树形形成方式可将其分为自然生长树形和人工培育树形。自然生长树形是由树体自身的分枝特性决定,未经人工整形修剪形成的树形。这类树形是由其遗传基因控制,因此不同种属间差异较大。常绿果树和落叶果树的自然生长树形存在差异:以柑橘^[18]为代表的常绿果树,在年生长周期中抽生新梢次数较多,易形成圆头形;而落叶果树如香梨^[19]的自然生长树形则为开心形。近年来,从自然芽变品种中筛选出的柱状苹果树因树体表现出矮化、枝条紧凑、分枝短等特点,被用来作为苹果矮化育种的重点研究对象。这类树形的结构特点是没有明显的主枝,在主干上直接着生10~12个结果枝组,上下错落着生。研究者对柱形树形的叶片解剖结构进行观察,发现柱形树形叶片中每一层的栅栏组织厚度均显著高于普通树形,且栅栏组织层数比普通树形少1层(柱形有2层,普通树形有3层)^[20]。也有研究发现柱状树形的枣树适合密植,且水分利用率较高,是枣树的节水丰产树形^[21]。

自然生长树形的形成和维护较简易,却较大幅度地降低了果园的生产效益。孙桂丽等^[19]研究发现,与疏散分层形相比,自然开心形对外界环境的敏感性不高,不易通过改善其生长的环境条件来提高光合速率。也有研究者发现,苹果自然主干形的病害较改造树形严重^[15]。当然这类树形在植株生长期间仍具有一定的优势。自然圆头形的枇杷可增强幼树生长势,利于幼树快速成形^[22]。Miller等^[23]也发现对桃树幼树进行修剪,会导致树体生长过旺,建议幼树应保持其自然生长状态。此外,研究者还发现自然开心形桃树的果实产量高于修剪树形,而且前者冠层不同部位果实的可溶性固形物含量也较高^[24]。迄今,人们已经对各种果树树形进行了比较研究,并针对不同种类和不同栽培地区筛选出了适宜推广应用的树形(表1)。

2 树形形成与调控的机制

2.1 调控树形形成的分子机制

近年来,关于木本植物树形形成的分子机制研究较多,大多集中于冠层分枝与节间长度遗传特点、矮化基因表达调控等方面^[25-27]。有研究发现多年生植物的冠层分枝特性是可遗传性状^[28]。也有研究发现苹果的节间长度是高度遗传的性状,且其遗传变异与细胞数目呈显著相关^[29]。Lu等^[27]获得了一个半矮生型桃变异单株,进一步研究发现该性状由显性单基因控制,温度调控节间长度并决定株高,通过图位克隆的方法精细定位了目标基因。Conner等^[30]利用分子标记方法探讨了与苹果树形态相关的数量性状位点QTL之间的关系。Knäbel等^[31]利用QTLs首次将梨的矮化基因与开花性状结合。Hollender等^[25]则在研究桃矮化性状基因*GID1*时,比较了*GID1*同源基因(*PpeGID1c*和*PpeGID1b*)的表达,发现*PpeGID1c*通过发夹结构导致基因沉默,且*PpeGID1c*沉默程度与矮化性状程度呈正相关。因此,对*PpeGID1c*的表达修饰既可以出现矮化性状,同时也不会对果实品质造成影响。You等^[32]还在苹果中发现dsRNA结合蛋白MdDRB1通过调节miRNAs及其靶基因的转录水平影响树体分枝特性,并确定了MdDRB1以保守的方式参与miRNA的形成。

砧穗互作已成为当前的研究热点之一。因嫁接是果树繁殖的重要途径,砧木和接穗的特性均会影响嫁接后果树的生长发育。其中,矮化砧木的致矮

表 1 不同种属果树的树形类型

Table 1 Tree shapes between some different kinds of fruit trees

品种 Cultivars	树形 Tree shape	适宜树形 Appropriate tree shape	品种 Cultivars	树形 Tree shape	适宜树形 Appropriate tree shape
富士苹果 ^[33] <i>Malus domestica</i> Borkh. Fuji	三主枝疏散分层、高干开心形 Three branches evacuation layered shape, Senior cadre open-center shape	高干开心形 Senior cadre open-center shape	葡萄 ^[43-45] <i>Vitis vinifera</i> L.	Y 型架、篱架、FI 树形、多主蔓扇形、厂字形 Y frame, Vertical trellis shape, FI tree form, Fan training system with multiple trunks, Slope trunk with a vertical shoot positioning training system	Y 型架、FI 树形、厂字形 Y frame, FI tree form, Slope trunk with a vertical shoot positioning training system
长富 2 号 ^[34] Naganofuji No. 2	三主枝开心形、四主枝开心形、五主枝开心形、自由纺锤形 Three branches open-center shape, Four branches open-center shape, Five branches open-center shape, Freedom spindle shape	三主枝开心形 Three branches open-center shape	杧果 ^[46] Mango	纺锤形、开心形、圆头形 Spindle shape, Open-center shape, Round shape	开心形 Open-center shape
玉华早富 ^[35] Yuhua precocious Fuji apple	V 形、Y 形、自由纺锤形、细长纺锤形、高纺锤形、改良纺锤形 V-shape, Y-shape, Freedom spindle shape, Slender spindle shape, High spindle shape, Improved spindle shape	V 形 V-shape	沙田柚 ^[46] Shatian pumelo	纺锤形、开心形、圆头形 Spindle shape, Open-center shape, Round shape	纺锤形 Spindle shape
短枝红富士 ^[36] Fuji apple trees	自由纺锤形、小冠疏层形、低干开心形 Freedom spindle shape, Small and sparse canopy shape, Low trunk open-center shape	低干开心形 Low trunk open-center shape	龙眼 ^[46-47] <i>Dimocarpus longan</i> Lour.	纺锤形、开心形、圆头形 Spindle shape, Open-center shape, Round shape	纺锤形 Spindle shape
红富士、乔纳金、王林和新红星 ^[37] Red Fuji, Jonagold, Orin and Starkrimson	直立中央领导干树形 Vertical axis shape	直立中央领导干树形 Vertical axis shape	毛叶枣 ^[12,46] <i>Zizyphus mauritiana</i> Lam	纺锤形、开心形、圆头形 Spindle shape, Open-center shape, Round shape	纺锤形 Spindle shape
新高梨 ^[38] <i>Pyrus pyrifolia</i> L.	Y 形、T 形、V 形 Y-shape, T-shape, V-shape	V 形 V-shape	梨枣 ^[21] <i>Zizyphus zizyphu</i>	Y 字形、柱形、开心形、自然圆头形、立壁式 Y-shape, Columnar shape, Open-center shape, Natural round shape, Vertical shape	柱形 Columnar shape
湘南梨 ^[39] <i>Pyrus pyrifolia</i> Nskai. Xiangnan	单层开心形、双层开心形、小冠疏层形 Single open-center shape, Double layered open-center shape, Small and sparse canopy shape	单层开心形 Single open-center shape	鲁枣 2 号 ^[48] Chinese jujube Luzao 2	小冠疏层形 Small and sparse canopy shape	小冠疏层形 Small and sparse canopy shape
鲜黄梨 ^[40] <i>Pyrus pyrifolia</i> Sunhwang	Y 字形、V 字形、平棚形、疏散分层形 Y-shape, V-shape, Flat frame shape, Evacuation layered shape	平棚形 Flat frame shape	桃 ^[4,23] <i>Prunus persica</i> L.	圆柱形、直立形、标准形、Y 形 Columnar canopy shape, Vertical shape, Standard shape, Y-shape	圆柱形、直立形、Y 形 Columnar canopy shape, Vertical shape, Y-shape
黄金梨 ^[41] <i>Pyrus pyrifolia</i> Hwang kumbae	棚架形 Frame shape	棚架形 Frame shape	油桃沪油 004 ^[49] Nectarine var. Huyou 004	主干形、Y 形、开心形、十字形 Trunk shape, Y-shape, Open-center shape, Cross shape	主干形 Trunk shape
安茹梨 ^[7] <i>Pyrus communis</i> L.	开心形 Open-center shape	开心形 Open-center shape	脆桃 ^[24] Bayuecui peach	主干形、开心形、主干形、开心形、 Trunk shape, Open-center shape	主干形 Trunk shape
库尔勒香梨 ^[19] Kuerle Xiangli	自然开心形、疏散分层形 Natural open-center shape, Evacuation layered shape	疏散分层形 Evacuation layered shape	锥栗 ^[50] <i>Castanea henryi</i> Rehd. et Wils	开心形、小冠疏层形、自然圆头形 Open-center shape, Small and sparse canopy shape, Natural round shape	开心形 Open-center shape
丰水梨 ^[42] Hosui	棚架形、疏散分层形 Frame shape, Evacuation layered shape	棚架形 Frame shape	樱桃 ^[51] Selah cherry trees	改良型篱壁式 The modified upright fruiting offshoots	改良型篱壁式 The modified upright fruiting offshoots
西洋梨 ^[3] <i>Pyrus communis</i> L.	纺锤形、V 形、双轴树形 Spindle shape, V-shape, Bi-axis shape	V 形、双轴树形 V-shape, Bi-axis shape	猕猴桃 ^[52] <i>Actinidia deliciosa</i> Hayward	篱架形 Vertica trellis shape	篱架形 Vertica trellis shape
			枇杷 ^[22] <i>Eriobotrya japonica</i> (Thunb.) L.	自然圆头形、渐开心形、层形、主干形、稀冠圆头形 Natural round shape, Gradually open-center shape, Layered shape, Trunk shape, Dilute the crown round shape	自然圆头形 Natural round shape
			温州蜜柑 ^[18] <i>Citrus unshiu</i> Marcow	自然圆头形、开心形 Natural round shape, Open-center shape	开心形 Open-center shape

现象,有人认为是由于抑制了赤霉素前体的合成,以致无法促进枝条生长^[53]。Xu等^[54]证实了苹果半矮化砧木的GAI (gibberellic acid insensitive) mRNA可长距离运输至接穗从而实现矮化的目的。此外,也有砧木调控开花生理、光合生理、抗病生理以及激素的信号转导机制的相关报道^[51,55]。日本研究者还采用多株树嫁接在一起的曲枝树形(joint tree training system),达到矮化、促花芽分化、早熟和高产的目的,并发现在花芽发育过程中,分生组织中的GA合成基因*PslGA3ox*表达量下降,*PslGA3ox*表达水平与IAA、GA活性呈正相关并控制花芽发育^[60]。

Zhang等^[57]证实*Co*是控制柱形树形成的关键基因,*Co*显性等位基因位于10号染色体上,以杂合的(*CO/co*)或纯合的(*CO/CO*)状态存在。此外,Bai等^[58]采用RNA-Seq、Microarrays和qRT-PCR等方法完成了*Co*基因差异表达检测,确定了*Co*的3个候选基因*mdlbd1~3*。利用SSR标记辅助选择柱形基因则发现*29f1-JW11r*等位基因仅在柱状型苹果中扩增,因此*29f1-JW11r*将可能是柱型苹果有效的筛选标记^[59]。Petersen等^[60]利用非柱状、杂合和纯合柱状苹果的根进行RNA-seq研究还发现,3者间*dmr6-like*基因在纯合子中表达显著上调,而在杂合基因型中下调,这说明利用此基因的表达量来进行柱形苹果的早期筛选也是可行的。此外,*IGT*被证实是调控柱形桃分枝角度的基因,而且柱状树形形成很可能是由于该基因调控植株顶端生长素的结果^[61]。

2.2 调控树形的激素机制

在基本树形形成的基础上,营养枝和结果枝的分枝角度、分枝方向、枝条数量及比例等决定了不同树形的冠层结构及特性,当不同枝条类型搭配适当,不同长度的枝条保持一定比例,且结果枝合理分布,连年形成健壮新梢和足够的花芽,才能保证树体优质高产稳产。已有研究表明,生长素和细胞分裂素含量及比例会影响枝条类型构成^[53]。马海燕^[62]发现葡萄新梢萌发与停止生长期,新梢生长的快慢等均取决于(GA₃+IAA)/ABA值。因此,生产中常通过喷施或涂抹生长调节剂调节冠层分枝特性。王磊^[63]通过对不同株型桃树枝叶内源激素不同时期的观测发现,7月垂枝型枝条上侧GA、IAA、ZR含量明显高于下侧,而ABA含量为枝条上侧低于下侧,从而使其生长速度低于中部上侧,枝条发生弯曲。还有一些激素可能是通过调控顶端优势控制植物株型,如

独角金内酯、赤霉素^[64]。而植物内源激素的平衡是调控树形形成的重要因素之一^[65]。研究者发现,在柱状和非柱状苹果的发育过程中,16种激素合成有显著差异^[66],Bendokas等^[67]证实IAA含量和IAA/ZT值偏高是柱状苹果幼树和结果树的共同特征。

不仅植物内源激素影响树形的形成,施用植物生长调节剂也能调控树形。研究者已发现外源独角金内酯(GR24)对苹果幼苗的形态建成有一定的影响:去除平邑甜茶顶芽后,GR24能够直接抑制侧芽的生长,同时能够减少地下部分主根长度、根毛数量和侧根数量^[68]。现今,果园中常使用多种生长调节剂混合配置,如由6-苄基嘌呤和赤霉素GA₄₊₇等比例混合配成的普洛马林,这类外源生长调节剂可提高氮素营养吸收、增加幼苗的干物质积累和分配,影响幼树翌年的形态建成^[69]。王兴静^[70]研究结果显示,在一定浓度范围内,植物生长调节剂组合浓度越高,越利于梨幼树萌芽抽枝。

3 人工整形修剪技术

3.1 不同果树的整形修剪

不同果树根据应用的树形不同,所采用的整形修剪方式有较大的差异。猕猴桃打顶对果实的形态和内部品质均有提高^[52],而苹果顶端修剪会使其果实变小^[8]。魏钦平等^[71]将‘富士’苹果小冠疏层形按春季一次整形和连续两年春季整形的方法,培养出高干开心形树形,发现一次性修剪由于枝梢修剪量大,较两年改形树体光照条件好。而黎德荣^[72]认为枇杷改造开心形树形需逐步回缩,修剪量过大会由于光渗透过多而引起日灼,建议每次修剪量最好不超过全树的1/3。树体分枝特性造成不同种属果树修剪效应的差异,董然然^[35]研究发现,为提高幼树早期产量和品质,‘皇家嘎拉’和‘富士’宜分别选用高纺锤形和V形。

高纺锤形苹果丰产园的冠层分枝特性为:总枝量为每hm²110万条,长枝、中枝、短枝的数量比约为1:1:8^[73]。李先明等^[39]发现‘湘南梨’小冠疏层形垂直高度2.5 m以上的部位为无产量效能的空间。提出小冠疏层形进行整形修剪原则应为:控制上层的直立枝和中部的侧枝长度,缩放下部侧枝,扩大下部的结果范围。也有人通过观察冠层特性指标,制定了冠层郁闭的临界条件,当树体冠层达到或超出这些值,则该考虑进行果树的整形修剪或间伐。尚志

华等^[74]将冠层相对光照强度<30%所占比例超过47.62%、生长季枝(梢)总量每hm²超过121万条和树冠内膛枝(梢)比例小于10%作为改良高干开心形‘富士’苹果冠层郁闭的3个临界指标。鲁韧强等^[75]通过建立果实品质指标与冠层相对光照强度之间的回归方程,得出‘瑞蟠5号’桃优质生产的最低条件是保证冠层相对光照强度达到34%,并依据冠层的光照条件,提出了有效树干体积的概念。

3.2 不同树龄果树的整形修剪

不同树龄果树的适宜树形有一定的差异。研究证实不同树龄的果树生长势不同,导致光合性能和产量有差异^[19]。幼树树形培养主要以快速形成树冠、提早开花为目的,进入结果期后则以维持丰产、稳产、优质、抗逆的树形为目标。如研究发现桃树过早的整形修剪,会导致枝条活力过高^[23]。王建新等^[34]发现低干开心形梨树只在初果期产量较高,进入盛果期后,高干和中干开心树形在产量上优势较明显。薛进军^[47]对龙眼的高产树形进行筛选时,发现纺锤形只在早期出现丰产性状,结果初期花量和果量均高于开心形和圆头形。但连续结果2 a后,开心形的产量却要优于其他2种树形。梁海忠等^[76]发现进入盛果期几年后的高纺锤形苹果,应及时疏除基部弱枝,同时短截更新,培养新的主枝。

3.3 整形修剪技术

断顶、拉枝、环剥、刻芽等是传统的整形修剪技术,近年来整形修剪又有了较大发展:(1)多种修剪方法配套实施:Mcfadyen等^[77-78]证实了修枝会降低常绿果树澳洲坚果枝条的碳水化合物含量,致使落果率增加,产量下降,而将修枝与环剥相结合时,则可显著缓解由于修剪所导致的落果现象。李雪薇等^[79]发现将‘富士’苹果拉枝后进行刻芽、扭枝和去顶梢的综合处理是较为有效的促花措施。(2)嫁接砧木:随着乔化果园逐渐被矮化密植果园所替代,矮化砧木逐渐成为人们的选择对象。M₂₆、M₉、GM₂₅₆等矮化砧木常被用作苹果自根砧和中间砧以形成矮化树冠^[76]。不同砧木对枝条分枝特性有影响,也会存在种属间的差异^[77],因此筛选不同嫁接砧木对砧穗亲和性、嫁接树体生长势乃至适宜树形形成等具有一定的作用^[53,80]。(3)调节叶果比:是实现库源之间同化物优化分配的重要途径。有研究者发现,短枝型植株的寿命受库源平衡的影响较大,当源不足以满足库的需求时,短枝存活率会下降^[81];Agnaldo等^[82]发

现,过大的果实负载极易导致枝条枯死,因减少了光合面积,使碳水化合物降低。Usenik等^[83]发现高密度的甜樱桃果园通过手动疏果可以增加叶果比,而叶果比越高,成熟期越早且果实品质越好;未经疏果处理的果树叶果比较低,会延迟果实成熟期。也有人发现不同水平的叶果比,碳水化合物积累、N元素的积累以及光合驯化方式和机制有差异,低水平的叶果比光合效率较高^[84]。(4)根系修剪:由于果树根系分布于地下深处,因此造成了对根系研究的局限性。断根是研究根系修剪的常用方法,Wang等^[85]发现进行根系修剪后的果树,叶水势、叶片膨压、气孔导度以及木质部离子浓度显著降低,木质部ABA含量显著高于未进行根系修剪的树体,表明根系修剪降低水分和养分的吸收是根系修剪抑制地上部分的营养生长和生殖生长的生理机制。Contador等^[86]运用非破坏性微根窗技术探究根系生长过程,研究结果显示冠层修剪会促进浅根系的生长,这可能与碳水化合物的竞争抑制根系的垂直生长有关。Emmett等^[87]采用分层取样获得根系,之后用WinRHIZO根系分析系统和ImageJ图像处理软件进行根系测量,获取了根系的解剖结构、生长顺序和轨迹,这为根系的进一步研究提供了新思路。(5)机械修剪:江才伦等^[88]在评估4种人工修剪方式的生产效益时发现,精细修剪分别比开大窗回缩修剪、开门修剪及对照的效益高19.70%、46.37%和131.43%,但精细修剪技术要求较高,无法满足果园大面积的修剪,只适合生产精品水果。在当前人力资源费用逐渐增加的条件下,机械修剪成为了国内外的发展趋势,但机械修剪目前仍需人工修剪来完善和实现冠层内部的光渗透^[13]。如何识别被修剪的枝条,提高识别传感技术,更好地优化修剪旺盛的营养枝,保留结果枝的修剪体系^[89]以及如何修剪出适宜肥药机械喷施的树形^[90]均是目前机械修剪的重点和难点。

4 树形的培养与维护

果树整形修剪措施应与产区气候环境条件相结合,二者之间存在相互反馈调节的关系,树形改造利于提高树体对生长环境的适应性,同时新的环境也对树形的选择有一定要求。因此,果树生产应在考虑省时省力的前提下,形成与不同树形相配套的果园群体管理措施。生产中,果树群体管理要以充分利用土地资源、提高群体光能利用率、增加果园整体

收益为主要目的。栽植密度影响果园的群体结构,决定了果园覆盖率及整个果园的通透条件,从而影响果园的经济效益。已有研究表明栽培密度应结合果树分枝特性、果园朝向等多种因素进行考虑^[11,91]; Badiu 等^[92]发现苹果的超密植园较密植园和疏植园效益更好。然而 Trentacoste 等^[93]研究发现栽植密度在一定范围内越稀疏,越能保证连年丰产。Widmer 等^[94]也发现‘皇家嘎拉’‘金冠’2个苹果品种的单株产量均随着种植密度的增加而减少。间伐是调节果园密度的常用方法。徐芳杰等^[95]通过隔行间伐改善高龄橘园的果实品质,并显著提高其抗树脂病能力。李培环等^[96]比较了苹果不同间伐方式的果园生理生态效应,发现隔行间伐程度大,果园生产恢复较慢,会影响整个果园的经济效益,行间隔3去1间伐恢复较快,起不到间伐效果。张列梅等^[97]研究发现,苹果 666.7 m²栽植 33~55 株,宜采用小冠开心形;超过 55 株,宜用纺锤形。

近年来,随着设施栽培逐渐普及与推广,一方面对减少自然灾害、改变物候期、提高肥水利用率、果品提质增效等有重要意义;另一方面,由于温室空间的限制以及覆盖材料对太阳光的反射和吸收,给树形研究提出了新思路。冯孝严等^[98]考虑到温室的群体效应,建议在前低后高温室大棚内,在不同高度的空间选择不同树形:空间大处选择主干形,低矮处选 Y 字形、开心形等树形。杨晓盆等^[99]发现葡萄棚架树形比篱架形更适合温室栽培,秦国新等^[44]提出了适合温室栽培的葡萄树形 FI 形,能显著改善光照条件,促进花芽分化,提高果实品质并保证连年丰产稳产。高清华等^[49]发现设施栽培条件下的主干形的油桃幼树在树冠形成早期光截获能力较高。

树形培养的果园,需要加强肥水促控,施足基肥,如苹果、梨秋季 666.7 m²施有机肥 3 000 kg 以上,以提高树体营养。果园水分的管理,需根据果园墒情而定,一般全年灌水 3~4 次^[100]。花果管理技术是果园实现优质高效生产的关键措施,需通过周年修剪调节花量,科学疏花疏果,合理负载。管好花果生长发育的每个环节,如果实套优质纸袋、地面铺反光膜、摘叶转果、及时防治病虫害等,对果实产量和果品质量均可起一定作用^[101]。

5 问题与展望

树形培养和维护是一个长期而繁复的过程,如

何正确地选择与评价适宜树形依然值得继续研究。但树形培养对不同果树的花芽分化、坐果率、产量及品质影响的一致性尚待商榷,这可能与被修剪果树种属间的特性和修剪树形评价时间有关。树形培养不是一个独立的栽培环节,树形成形后需分析不同整形方式相应的生理生态条件;确定不同树形树体的水肥吸收及利用情况,针对性地制定不同树形相应的水肥管理体系。此外,树形培养的经济效益不可忽视,机械修剪虽取得了较多成果,但对树形的识别方面仍需继续开发。还可考虑调节果园群体的分布,进行间作或套作,实现果园资源的高效利用,提高单位面积的经济产量。

树形形成与调控的机制,目前已在桃、苹果、梨中筛选出树形矮化和半矮化的调控基因,但其对于网络调控的机制尚不十分明确,而且其他果树矮化新种质的创制和新品种的培育十分迫切,从基因和分子生物学层面挖掘树形调控基因、揭示树形形成机制将会是树形研究的重要方向。

总之,良好的冠层结构是果树高产优质的基础,适宜树形是果树规模化、产业化的保障,果树整形修剪往往需要数月甚至连续几年时间才能表现出修剪效应,极不利于人们对整形修剪方法进行及时评估与矫正;而且在复杂的果园小气候环境下,研究者也很难对不同树形,尤其是交互作用因子间做出真实客观的评价。因此,借助数学模型和计算机辅助量化的方法评价树形将会成为今后树形评价的有效途径。

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