Mechanics and morphology of permanent attachment systems in plants

Zur Erlangung des akademischen Grades **Doktor der Ingenieurwissenschaften**der Fakultät für Maschinenbau der Universität Karlsruhe (TH)

genehmigte

Dissertation

von

Dipl.-Biol. Tina Luise Hanna Steinbrecher

aus Speyer

Tag der mündlichen Prüfung: 01.04.2010 Hauptreferent: Prof. Dr. Oliver Kraft Korreferent: Prof. Dr. Thomas Speck

> Institut für Materialforschung II Forschungszentrum Karlsruhe

> > Karlsruhe 2010

Schriftenreihe Werkstoffwissenschaft und Werkstofftechnik

Band 72/2011

Tina Steinbrecher

Mechanics and morphology of permanent attachment systems in plants

Shaker Verlag Aachen 2011

Bibliographic information published by the Deutsche Nationalbibliothek

The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available in the Internet at http://dnb.d-nb.de.

Zugl.: Karlsruhe, Karlsruher Institut für Technologie, Diss., 2010

Copyright Shaker Verlag 2011

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior permission of the publishers.

Printed in Germany.

ISBN 978-3-8322-9923-1 ISSN 1439-4790

Shaker Verlag GmbH • P.O. BOX 101818 • D-52018 Aachen Phone: 0049/2407/9596-0 • Telefax: 0049/2407/9596-9

Internet: www.shaker.de • e-mail: info@shaker.de

Abstract

Permanent attachment pads of climbing plants are an example of highly efficient attachment structures, which have been evolved, tested and optimized in the course of evolution. However, information about the attachment mechanisms is still scarce, although the excellent mechanical performance of attachment structures has been recognized. In this study, the morphology and the biomechanics of attachment pads of Boston Ivy (*Parthenocissus tricuspidata*) as well as the interface between the pad and different substrates were investigated. The self-clinging liana *P. tricuspidata* develops swollen tips at the end of its tendrils which form into attachment pads. Attached and non-attached structures were analyzed using microscopical and mechanical testing methods. The overall strength of the interface was studied using tensile tests on a large number of individual pads attached to different substrates. On the micrometer-scale, the mechanical properties of the constituent materials were studied using nanoindentation.

Ontogenetic variations in the morphology of attached and non-attached structures were observed. Cell size, cell orientation and grade of lignification vary over the pad cross-section normal to the interface. Furthermore, cell size, cell wall thickness as well as cell orientation show variations in the plane of the interfacial region. The cells in the edge regions appear to secrete a strong adhesive fluid. The morphological variations are related to changes in mechanical properties. For example, the region close to the pad edge is up to four times stiffer than the regions closer the pad center.

A single lignified pad withstands normal stresses at the interface of up to 4 MPa while failure never occurred only at the interface. Four different failure modes were observed: failure of the substrate, internal failure of the attachment pad, a combination of the two modes or in case of non-porous materials mixed failure of plant components and interface. The attachment strength of young pads has been found to be significantly smaller than the attachment strength of older, lignified pads. It was on average only 28% of the value found for the older pads. The attachment process can be described at least as a two step process with a pre-attachment and a final attachment. Microscopical investigations show a perfect form closure between pad and substrate. Overall, attachment structures of climbers can be considered as a composite material and these natural interfaces are promising models for new technological concepts.

I

Kurzzusammenfassung

Permanente Haftscheiben bei Kletterpflanzen stellen ein Beispiel für hocheffiziente pflanzliche Anhaftstrukturen dar, die die Natur im Laufe der Evolution entwickelt, getestet und optimiert hat. Obgleich die exzellente mechanische Leistungsfähigkeit biologischer "Werkstoffverbunde" bekannt ist, sind die zugrunde liegenden Strukturen der Grenzflächen, wie interne "Verschweißungen" und "verklebte" Grenzschichten, noch wenig beschrieben. Ziel dieser Arbeit ist es, die (Mikro)-Mechanik und Funktionsmorphologie permanenter Haftscheiben des Wilden Weins (*Parthenocissus tricuspidata*) sowie die Materialgrenzflächen zwischen der Haftscheibe und verschiedenen Substraten in einem interdisziplinären Ansatz zu untersuchen. Angehaftete und nicht angehaftete Strukturen wurden morphologisch und mechanisch charakterisiert. Die Haftkraft der Gesamtstrukturen wurde mit Hilfe von Zugversuchen bestimmt und die mechanischen Eigenschaften der einzelnen Gewebe durch Nanoindentation.

Während der Entwicklung der Haftstrukturen werden verschiedene typische Stadien durchlaufen. Voll ausdifferenzierte Haftscheiben weisen sowohl über den Querschnitt als auch über die Kontaktfläche diverse Gradienten auf. Zellgröße, Zellorientierung und Grad der Lignifizierung variieren über den Querschnitt. Die Kontaktfläche der Haftscheiben weist ebenfalls Variationen der Zellgröße, der Zellorientierung und der Zellwanddicke auf. Morphologisch kann ein innerer und ein äußerer Bereich auf der Kontaktfläche unterschieden werden, wobei in der äußeren Region ein Haftsekret sezerniert wird. Die morphologischen Änderungen resultieren in Änderungen der mechanischen Eigenschaften. Der äußere Bereich der Kontaktfläche ist zum Beispiel bis zu vier Mal so steif wie die inneren Regionen.

Zugversuche haben gezeigt, dass eine Haftscheibe Spannungen von bis zu 4 MPa standhält, wobei im Fall des Versagens die Haftscheibe niemals komplett vom Substrat getrennt werden konnte. Es traten vier verschiedene Versagensmodi auf: Versagen des Substrates, internes Versagen der Haftscheibe, teilweises Versagen des Substrates und der Haftscheibe, und im Fall von glatten Oberflächen ein teilweises Versagen von Komponenten der Haftscheibe. Die Haftkraft junger Haftscheiben ist signifikant geringer als die von älteren, lignifizierten Haftscheiben. Sie betrug im Mittel nur 28% des Wertes der für lignifizierte erreicht wurde. Die Anhaftung kann daher mindestens als 2-stufiger Prozess mit einer Voranhaftung und einer finalen Anhaftung verstanden werden. Untersuchungen der Materialgrenzfläche zeigen einen perfekten Formschluss zwischen der Haftscheibe und dem Substrat.

Danksagung

Die vorliegende Arbeit entstand zwischen September 2006 und Dezember 2009 am Institut für Materialforschung II des Forschungszentrums Karlsruhe. Ich möchte mich bei allen bedanken, die direkt oder indirekt zum Gelingen dieser Arbeit beigetragen haben. Bei Herrn Prof. Dr. Oliver Kraft möchte ich mich für die Übernahme des Hauptreferats und sein Interesse an meiner Arbeit bedanken sowie dafür, dass er mir die Möglichkeit gegeben hat diese Arbeit an seinem Lehrstuhl anzufertigen. Herrn Prof. Dr. Thomas Speck danke ich für die Übernahme des Korreferats, seine Unterstützung und Diskussionsbereitschaft und Frau Dr. Ruth Schwaiger für die Betreuung der Arbeit.

Ein herzlicher Dank gilt Herrn Dr. Günter Beuchle für seine stete Hilfsbereitschaft und kompetente Unterstützung bei der Anfertigung der ESEM-Aufnahmen.

Ein ganz besonderer Dank geht an meine Mitdoktoranden sowie alle Mitarbeiter des Institutes für die außerordentlich gute Zusammenarbeit. Diese Arbeit wäre ohne ihre Hilfe nicht möglich gewesen, wofür ich mich bei allen herzlich bedanken möchte. Insbesondere danke ich der Abteilung Biomechanik für ihre Anregungen und ihre konstruktive Kritik sowie Sofie Burger, Christian Dethloff und Benjamin Völker für die tatkräftige Unterstützung und sorgfältiges Korrekturlesen der Arbeit.

Bei der Plant Biomechanics Group Freiburg möchte ich mich für die gute Kooperation und Bereitstellung von Messapparaturen und insbesondere bei Katrin Seidelmann und Björn Melzer für ihre Hilfe bedanken.

Nicht zuletzt möchte ich meinem Bruder und meinen Eltern danken, die mich in jeglicher Hinsicht unterstützt haben.

Table of Contents Abstract ı Ш Kurzzusammenfassung V Danksagung ΙX List of figures List of tables XVII Introduction 1 2 Basic Principles and Literature Review 5 Biological materials and structures 5 2.2 Permanent attachment systems in climbing plants 7 2.3 Mechanical testing of biological materials and structures 9 2.4 Nanoindentation of biological materials and structures 12 Materials and Methods 15 3.1 Plant Material 15 15 3.1.1 Climbing Plants 3.1.2 Substrates 17 3.1.3 Microscopy and staining 18 3.2 Experimental details 19 19 3.2.1 Tensile testing 3.2.1.1 Tensile testing apparatus 19 3.2.1.2 Sample preparation 23 3.2.2 Nanoindentation 25 Results 31 4.1 Morphological and anatomical analysis 31 4.1.1 Morphology of the searching shoot 32 4.1.2 Development of the attachment structure 32

Table of Contents

		4.1.3	Topology of the interface	37
		4.1.4	Characterization of the microstructure	40
		4.1.5	Shape optimization and stress distribution	44
	4.2	Biome	echanical investigation	47
		4.2.1	Tensile Tests	47
			4.2.1.1 Individual mature attachment pads	47
			4.2.1.2 Comparison of juvenile and adult pads	54
			4.2.1.3 Tensile tests on complete attachment structures	56
	4.3	Nanoi	ndentation	59
5	Disc	ussior	n	63
	5.1	Attach	nment process and ontogenetic variations in morphology	63
	5.2	Struct	ural gradients in the attachment pad and form optimization	66
	5.3	Corre	ation between mechanical properties and morphology	72
		5.3.1	Attachment strength and failure modes	72
		5.3.2	Comparison of young and lignified attachment pads	75
		5.3.3	Complete attachment structures	76
		5.3.4	Mechanical properties of the constituent materials	80
		5.3.5	Mechanical properties of interface and microstructure	81
6	Sun	nmary a	and Outlook	85
Α	Арр	endix		89
	A.1	Growt	h conditions in phyto-chamber	89
	A.2 Brief overview of the theory of nanoindentation			
Re	feren	ces		95

List of figures

- Figure 2.1: Material property chart plotting Young's modulus E against 10 density ρ. The heavy envelopes enclose data for a given class of material. The guidelines of constant E/ρ, E^{1/2}/ρ and E^{1/3}/ρ allow to identify structurally efficient materials which are light and stiff (after [106]).
- Figure 3.1: Permanent attachment structures of Boston ivy (*P. tricuspidata*). 16 (a) The self-clinging species covers the whole supporting wall in the Botanical Garden at the University of Freiburg. (b) Plant axes with attachment structures. (c) Complete attachment structure consisting of nine attachment pads. (d) Lignified attachment pad.
- Figure 3.2: Tensile testing machine. (a) Mobile tensile tester placed on a ball 20 ended tripod. A support rod in contact with the structure the plant is growing on is used to stabilize the tripod. (b) Schematic of the tensile testing device. A load sensor and a displacement sensor are positioned on a linear unit with spindle drive while a motor mediates smooth movement. At the load sensor there is a bore hole for the installation of the grip device (tweezers).
- Figure 3.3: Determination of the influence of a misalignment angle during the 21 tensile test. The resulting force of a defined mass was measured under different misalignment angles α .
- Figure 3.4: Decrease in the force measured F_{meas} against the misalignment angle α . The force values were normalized by the maximum value measured at $\alpha = 0^{\circ}$ misalignment. At a 0° misalignment, F_{meas} equals the applied force F_{appl} . The greater the misalignment angle α , the greater the systematic error. Misalignment of up to 5° results in an error of approximately 2° which was considered acceptable for the experiments (indicated with an arrow). The theoretical decrease of the measured force $F_{theor} = F \times \cos(\alpha)$ is plotted for comparison.
- Figure 3.5: Stainless medical tweezers as grip devices for the attachment 24 structures. Depending on the shape of the structures and their positions the appropriate tweezers were selected. (a) Tweezers with 1:2 ratio of interlocking teeth. (b) Tweezers with 1:2 ratio with delicate teeth for small samples. (c) Tweezers with a 2:3 ratio of interlocking teeth. (d) Double-rowed tweezers.

- Figure 3.6: (a) Two attachment pads with applied glue droplets. Flat samples 25 like individual attachment pads of *P. tricuspidata* could not be held with tweezers without being damaged. To ensure a firm sample-tweezers connection glue droplets were put on the attachment pads. At the pad edge clear indications of an adhesive substance secreted by the plant can be seen. (b) Schematic of experimental setup. A glue droplet is applied on the pad. The tweezers grab the glue droplet and the force is applied in the normal direction to the substrate.
- Figure 3.7: Schematic of the indentation system. The force generating system consists of a coil/magnet assembly. The displacement measurement is achieved by a parallel plate capacitor. The system measures the penetration of a tip into the sample. The sample is positioned by a piezo driven x-y sample tray.

26

- Figure 3.8: (a) Schematic force-displacement curve for wood cells with 28 (1) loading, (2) peak hold, (3) unloading, (4) hold segment to determine the thermal drift (4) and final unloading (5). (b) Corresponding indentation displacement-time curve (after [206]). The increasing penetration depth during the hold (2) indicates time-dependent deformation.
- Figure 3.9: Sample preparation for nanoindentation tests. (a) Section of an 29 attachment pad. Tests were conducted within the cross-sectional cut perpendicular to the attachment surface. (b) Detached pad from gelatine. Tests were conducted on the attaching surface.
- Figure 4.1: Schematic of the attachment process. Showing the transition 31 from a juvenile attachment pad to a lignified attachment pad.
- Figure 4.2: Morphology of the searching shoot of *P. tricuspidata*. 33 (a) Searching shoot with a bent tip. (b) Micrograph of a searching shoot. The shoot surface is covered with small hooks (ESEM, 20 kV, 120 Pa). (c) Micrograph of a hook. The hook surface shows a pattern of protrusions (ESEM, 20 kV, 120 Pa). (d) Micrograph of shoot surface hooks. The hook base is made up of socket cells (ESEM, 20 kV, 120 Pa).
- Figure 4.3: Micrograph of a developing attachment pad (ESEM, 20kV, 3-120 Pa). (a) Tendril with swollen tip. (b) Upper part of a non-attached juvenile attachment pad. (c) Basal part of the swollen tip with a rough surface structure.

- Figure 4.4: Micrograph of a freshly attached pad on sponge rubber (ESEM, 10 kV, 120 Pa) (a) Top view of an attachment pad with the tendril shaft. (b) Detail of the edge of an attachment pad. Globular bulging cells form a well defined boundary with the substrate. (c) Schematic of the attachment pad: the cell size increases towards the edge and the pad forms a steep angle with the substrate.
- Figure 4.5: Optical micrograph of a cross-section through a lignified 36 attachment pad on a cardboard substrate. The contour is schematically indicated by the black line. The dashed line is the boundary between pad and substrate. The height/width ratio is approx. 1: 6.3.
- Figure 4.6: Micrograph of a lignified attachment pad (the cross-section is shown in Fig. 4.5) on a cardboard substrate (ESEM, 20 kV, 120 Pa).

 (a) Top view: the central part of the pad is surrounded by a wide seam. (b) Edge of the attachment pad exhibiting a rough surface with the appearance of entangled cells. (c) Tendril leading into the attachment pad.
- Figure 4.7: Micrograph of the bottom surface of a differentiated non-attached 37 pad (ESEM, 20 kV, 120 Pa). A central and a peripheral region can be distinguished.
- Figure 4.8: Micrograph of the bottom of an attachment pad removed from 38 gelatine. The central part of the attachment pad exhibits a cavity and is surrounded by globular cells. The peripheral part of the attachment pad shows elongated cells which form a ring of approx. 450 µm width (ESEM, 20 kV, 120 Pa).
- Figure 4.9: Micrograph of the contact surface of a detached lignified 39 attachment pad removed from gelatine (SEM, 5 kV, 10⁻⁶ Pa).

 (a) Curvature of the contact surface. (b) Peripheral region of the attachment pad. The cells are elongated and seem to be fused. (c) Tip of a peripheral cell probably covered with an adhesive fluid.
- Figure 4.10: Optical micrograph of a cross-section of a lignified attachment 40 pad on sponge rubber. The interface between plant and substrate has a curvature and the pores of the sponge rubber are filled with plant material.

- Figure 4.11: Optical micrograph of a cross-section of a stained attachment 41 pad on a birch wood substrate (stained with safranin astra blue).

 (a) Different lignified (red) and unlignified (blue) regions can be distinguished: a lignified central part (2), an unlignified interface layer (4) and an unlignified upper region (cap region) (1). (b) The plant fills the vessel elements of the wood and creates a perfect form closure with the substrate.
- Figure 4.12: Micrograph of a cross-section through an attachment pad on birch wood substrate (SEM, 5 kV, 10⁻⁶ Pa). (a) Lateral cells of the attachment pad are orientated at 45° to the substrate. (b) Interface layer between plant and wood substrate. The vessel elements of the wood are filled with an electron-dense material. Cells in the interfacial region seem to be collapsed.
- Figure 4.13: Comparison of a real attachment pad contour and a calculated 44 optimized geometry (shown as line overlay) constructed by the method of the tensile triangles [207] for two typical length/width ratios.

 (a) Length/width ratio of 1:2. (b) Length/width ratio of 1:1.3.
- Figure 4.14: Attachment pad geometry constructed by the method of the 44 tensile triangles [207] for two typical length/width ratios. (a) Length/width ratio of 1:2. (b) Length/width ratio of 1:1.3.
- Figure 4.15: Digitalized microtome section of an attachment pad on wood 45 substrate for a 3D model. The color coding is based on the original intensity of the colors of the microtome section.
- Figure 4.16: 3D model of an attachment pad on a wood substrate. The 46 model has been constructed from a sequence of images of microtome cut sections. The wood substrate with its xylem vessels is shown at the bottom. The sections shown are parallel to the tendril which can be seen on the left-hand side.
- Figure 4.17: Force vs. displacement for an individual attachment pad of 48 *P. tricuspidata* on plaster determined from tensile tests. The force was applied normal to the substrate and the pad was gripped with tweezers with teeth of specification 1:2. Failure occurred at 6.25 N.

Figure 4.18: Maximum attachment forces for different test substrates for 49 individual pads determined from tensile tests. The force was applied in normal direction to the substrate. The failure mode predominant for the substrate is indicated as S = substrate failure, PC = failure of plant components and interface, PC-S = failure of both plant components and the substrate.

Figure 4.19: Schematic of the failure modes observed in tensile tests.

50

52

Figure 4.20: Experimental observation of the failure modes of the plant/substrate attachment system. (a) Contact surface of an attachment pad pulled off plaster. The whole pad area is covered with parts of the substrate (failure mode 1). (b) Attachment pad torn into two parts. The upper picture shows the top, while the lower picture illustrates the remaining part on the substrate (failure mode 2). (c) Contact surface of an attachment pad pulled off plaster demonstrating the mixed failure mode. The edge of the attachment pad is covered with plaster while the central part of the attachment pad is ripped out and remains on the substrate (failure mode 3). (d) The outer seam of the attachment pad remained on the aluminum substrate whereas the central part of the pad became detached during the tensile test (failure mode 4).

Figure 4.21: Mean values of attachment force, attachment area and resultant 53 stress for different substrates. The error bar represents one standard deviation.

....t E4

Figure 4.22: Force vs. displacement for (a) an individual fresh attachment 54 pad (b) a lignified attachment pad on plaster.

55

Figure 4.23: Mean attachment strength of young, fresh attachment pads of *P. tricuspidata* on plaster compared to older lignified ones at the same growing site determined from tensile tests in direction normal to the substrate (sample number: n = 20 each). Old, lignified attachment pads withstand a mean force of 5.6 ± 3.0 N whereas young, fresh ones show on average only 28% of this value with 1.6 ± 0.8 N. The error bar represents one standard deviation.

- Figure 4.24: Typical force-displacement curves for attachment structures of *P. tricuspidata* consisting of several attachment pads. The force was applied parallel to the main tendril axis. The zig-zag pattern results from subsequent failure of either individual attachment pads or simultaneous failure of several pads as indicated by the numbers in the graph. Every steep load drop corresponds to one failure event. Maximum forces are indicated in the figures.
- Figure 4.25: Comparison between maximum forces of complete attachment 58 structures and individual attachment pads determined from tensile tests (sample number: $n_{complete} = 10$, $n_{individual} = 17$). The force was applied in the direction parallel to the main tendril axis in case of the complete attachment structures and normal to the substrate for individual attachment pads. The error bar represents one standard deviation.
- Figure 4.26: Force-displacement curve of the interface layer determined from 59 indentation with a flat punch tip of 20 µm diameter. Loading phase, hold segment and unloading phase are indicated in the graph. The strain rate was 0.05 s⁻¹; the peak hold time 30 s. Thermal drift was corrected.
- Figure 4.27: Mean values for the cross-sectional indentation modulus of the $\,$ 60 interface layer at different positions with a flat punch tip of 20 μm diameter. The error bar represents one standard deviation.
- Figure 4.28: Indentation modulus determined from indentation tests on 61 attachment pad surfaces with a flat punch tip of 20 µm diameter. The indentation modulus tends to increase from the center towards the edge of the pad.
- Figure 4.29: Indentation modulus of different tissues of a pad cross-section. 62 The unlignified upper region (cap region), the unlignified interfacial boundary layer and the birch wood substrate were tested with a flat punch tip with 50 μ m. The error bar represents one standard deviation.
- Figure 5.1: Micrograph of a contact-sensitive tendril of Bryony (*Bryonia* 64 *dioica*) with tactile plebs on the epidermal surface (SEM) (from [211]).
- Figure 5.2: Schematic of the development of an attachment pad of *P*. 65 tricuspidata. (a) Stage I: Undifferentiated centrisymmetric attachment pad.
 (b) Stage II: Beginning of differentiation: transformation from round to flattened shape. (c) Stage III: Differentiated attachment pad. (d) Stage IV: Mature lignified attachment pad surrounded by a seam.

- Figure 5.3: Schematic showing that the plant material is filling the pores in 67 the substrate, thereby achieving form closure.
- Figure 5.4: Schematic of the force application for two length/width ratios 69 1:2.5 and 1:6.3. It is assumed that the force is distributed in radial direction within the interfacial layer.
- Figure 5.5: Optical micrograph and schematic of the force application for two 70 length/width ratios 1:2.5 and 1:6.3. It is assumed that the force is distributed in radial direction within the interfacial layer.
- Figure 5.6: Schematic of the location of the highest stress concentration 71 (indicated with an arrow) for different attachment pad geometries and the resulting most reasonable fracture path. (a) Attachment pad without outer seam, e.g. fresh attachment pad. (b) Attachment pad with an outer seam.
- Figure 5.7: Influence of form closure and an adhesive on the failure modes 73 of attachment pad for (a) porous materials (b) non-porous ones. The white line indicates the failure mode (cf. 4.19).
- Figure 5.8: Influences of form closure and adhesive on the attachment to different substrates. Red color indicates the influence of the form closure and the adhesive whereas blue color indicates the influence of the adhesive. Cases where the substrate is the limiting factor due to substrate failure are indicated with an S. The maximum value for wood (birch and beech) shown in the figure represents a lower limit since in the majority of cases the glue-plant bonding failed.
- Figure 5.9: Schematic of the main axis of *P. tricuspidata* with two attachment 77 structures. Each attachment structure is composed of a coiled main tendril serving as a spring and several attachment pads.
- Figure 5.10: Determination of energy dissipation of the complete attachment 79 system. The total energy dissipated as derived from integration of the area under the force-displacement curve is 69.6 mJ. The energy dissipated during each step of the detachment is indicated as W₁, W₂, W₃, W₄, W₅. The third and the fifth peak represent failure of two attachment pads whereas all other peaks represent the failure of individual pads.

- Figure 5.11: (a) Typical force-displacement curve determined from 80 indentation tests (cf. 4.26). (b) Schematic force-displacement curve for wood cells with loading (1), holding (2) and unloading segments (3). (c) Corresponding indentation displacement-time curve (after [206]). The increasing penetration depth during the hold (2) indicates time-dependent deformation.
- Figure 5.12: Variation of the indentation modulus over the contact surface of 82 an attachment pad. The mean values over the center and edge regions are represented by dashed lines.
- Figure 6.1: Temperature and humidity in the phyto-chamber measured over 89 a period of 30 days by a Testo 175 Compact-Data-Logger.
- Figure 6.2: Schematic of an indentation showing parameters characterizing 91 the contact geometry for a Berkovich tip (after [159]). F = indentation force, h = total displacement of the indenter, h_s = displacement of the surface at the perimeter of the contact, h_c = contact depth, h_f = final depth after complete unloading, a = radius of the contact circle.
- Figure 6.3: Harmonic oscillators used to model the dynamic response of the nanoindentation system. (a) Dynamic response of the indenter head D_i , the support springs D_s , the load-frame stiffness K_f and the contact stiffness with a test sample S. (b) Model of the overall system described as a harmonic oscillator with the effective stiffness K, the effective damping D and the mass of the indenter shaft m. A sinusoidal force signal F(t) results in a displacement z(t) which lags behind by the phase angle δ .

List of tables

- Table 3-1: Growth conditions in the phyto-chamber. The chamber had a size of 2.5 m x 2.75 m with 2.1 m height. Light, temperature and humidity were adjusted automatically. Temperature and humidity were recorded by a data logger (see Appendix A.1 for more details).
- Table 3-2: Organic and inorganic climbing substrates presented to 17 $P.\ tricuspidata$. The roughness was determined from white light interferometry. R_a , R_q and R_z denote the arithmetic average roughness, the root mean squared roughness and the average distance between the highest peak and lowest valley in each sampling length, respectively [205].
- Table 4-1: Mean cell sizes over a cross-section of an attachment pad 41 (cf. Fig. 4.11) Data from 20 pads was collected; 10 cells per region were analyzed.
- Table 4-2: Mean and maximum forces and stresses from tensile tests of 49 pads with the force normal to the substrate on different materials. The scatter is represented by one standard deviation.
- Table 4-3: Frequency of the different failure modes for different substrates. 51
 The observed failure modes are stated in percent of the analyzed experiments. The experiments discarded because of failure of the methodology, e.g. failure of the glue/plant bonding are indicated in column 5.
- Table 4-4: Mean and maximum values for force F, displacement h and 58 energy W of complete attachment structures of *P. tricuspidata* from tensile tests (sample number n = 10).